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ALLOMETRY IN PTEROSAURS[1]

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Abstract—The bivariate allometric equation has been used to study the relation between size and shape in 16 taxa of pterosaurs ranging in mass from about 4 g to an estimated 75 kg. Measurements of various features are related to the mass, which reflects the overall size of the animal. Shaft diameters of wing and leg bones show positive allometry with respect to mass, a partial solution to difficulties of support. Increase in length of wing bones shows an orderly gradient ranging from positive allometry in the middle members to isometry in proximal and distal members. Length of tail and size of metacarpals of the Rhamphorhynchoidea and Pterodactyloidea exhibit contrasting patterns of allometry; tail length variation can be interpreted in terms of different stability in flight.

The allometry of wing surface area is positive relative to mass and that of wing loading is negative relative to mass. Pterosaurs show lower wing loadings than most other flyers of the same mass, although well within the range for birds and bats. Large pterosaurs, then, flew slowly and with a high degree of maneuverability. The change of wing shape in progressively larger pterosaurs produces lower coefficients of induced drag. The mass of *Quetzalcoatlus northropi,* the giant pterosaur from Texas, is estimated at 75 kg.

THE UNIQUE NATURE of the reptilian adaptation to flight seen in pterosaurs has generated much scientific and pseudoscientific speculation for over 150 years. Cuvier (1801) was the first to recognize pterosaurs as flying reptiles, although he did not publish full details until about eight years later. In fact, not all authors have endowed pterosaurs with the power of flight; Wagler (1830) reconstructed the wings as flippers used in swimming.

Pterosaurs also pose some major questions about size and shape because birds and pterosaurs exhibit the largest range of body sizes known in any group of flying organisms. The smallest pterosaurs are roughly the size of a sparrow while the largest, *Quetzalcoatlus northropi,* we judge to have had a wingspan of 11.43 m (Langston, 1980; personal communication, 1981) and a mass of about 75 kg. Unfortunately, it is not fully preserved (Lawson, 1975a, b), and its size has sparked a lively scientific debate. Various authors have estimated the wingspan from 5.25 to 21 m (Greenewalt, 1975a; Lawson, 1975a, b; McMasters, 1976). According to Langston, two large pterosaurs have been found in the Upper Cretaceous rocks of Texas. *Q. northropi* is the larger. A smaller animal, *Quetzalcoatlus* sp., has a wingspread somewhere between 5.5 and 6.7 m. By comparison, the postulated mass and wingspan of the largest flying bird, a Tertiary teratorn from Argentina, are approximately 80 kg and 6.4 m, respectively (K.E. Campbell, personal communication, February, 1981; see also Anonymous, 1980; Campbell, 1980; Campbell & Tonni, 1980). The mass of the biggest bat known to us is only 1.6 kg (McFarland & others, 1979).

Obviously, flying animals face an extreme functional problem because the area of the

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wing must be able to generate enough aerodynamic lift to support the weight of the entire body in the air. Our curiosity stems from the fact that adult pterosaurs were able to sustain flight over a wide range of sizes.

Inasmuch as the purpose of this paper is to study size and shape of mature pterosaurs in relation to flight adaptation, there is no need to review the vast taxonomic literature. Recent reviews of taxonomy and to some extent phylogeny and functional morphology were given by Saint-Seine (1955), Khozatsiy and Yurbev (1964), Müller (1968), and Wellnhofer (1970, 1975a, b, c, 1977, 1978). The adult pterosaurs are drawn from two different suborders, the Pterodactyloidea and Rhamphorhynchoidea, but except for the length of the tail and the metacarpal, the two groups can be treated as a single population. Rhamphorhynchoids are characterized by long tails and comparatively short metacarpals, whereas pterodactyloids have short tails and more elongate metacarpals (Wellnhofer, 1970, 1975a, b, c, 1977). Other differences in average proportions between the two suborders are not statistically significant, although this may reflect the small sample sizes for this study rather than the true situation. For example, the heads and necks of rhamphorhynchoids are typically shorter than those of pterodactyloids.

In view of the obvious problems of allometry and functional morphology, it is surprising how little statistical work has been done on pterosaurs. Some statistical observations have been presented on *Pterodactylus* by Wellnhofer (1970) and Mateer (1976) and on *Rhamphorhynchus* by Wellnhofer (1975b); these authors used somewhat different measurements from the ones discussed here, and their papers were confined to ontogeny and taxonomy of small taxonomic groups rather than all pterosaurs.

As one might expect, many interesting papers on pterosaurs deal with mechanisms of flight. The first appeared before the invention of the practical airplane (Dennis, 1861; Marsh, 1882; Seeley, 1901; Langley, 1902; Lucas, 1902). Inasmuch as pterosaurs included the largest flying animals known at that time, at least two of these papers were also concerned with solving the problems of powered flight (Langley, 1902; Lucas, 1902). In the four decades after the first successful man-carrying powered aircraft was flown by the Wright brothers in 1903, several papers were published on the aerodynamics of pterosaurs (e.g., Lull, 1906; Hankin & Watson, 1914; Short, 1914; Wiman, 1923, 1925; Kripp, 1943). Most of the recent literature on flight performance emphasizes such larger forms as *Pteranodon* (Bramwell & Whitfield, 1970, 1974; Bramwell, 1971; Heptonstall, 1971, 1972; Whitfield & Bramwell, 1971; Stein, 1975; Whitfield, 1979); recent papers have also discussed the size and possible flight capacity of *Quetzalcoatlus northropi* (Greenewalt, 1975a; Lawson, 1975a, b; McMasters, 1976; Stein, 1976; Langston, 1981). Smaller pterosaurs belonging to *Rhamphorhynchus* and *Pterodactylus* were considered by Wellnhofer (1970, 1975c). General reviews have been presented by Saint-Seine (1955), Wellnhofer (1978), Brower (1980), and Langston (1981).

Some knowledge about the mode of life of pterosaurs is necessary for appreciation of changes in size and shape. Most pterosaurs are known from marine and shoreline sediments. These animals probably exploited the same ecological niches as seabirds and shorebirds (Brown, 1943; Wellnhofer, 1970, 1975c, 1978; Bramwell & Whitfield, 1974; Langston, 1981; see Kaufmann, 1970 and Dorst, 1974 for general discussion of the ecology and flight of shorebirds and seabirds). A few pterosaurs including *Sordes* (Sharov, 1971) and *Quetzalcoatlus* (Lawson, 1975a; Langston, 1981), have been found only in nonmarine sediments. This incidence results from the likelihood of preservation rather than the original distributions, and pterosaurs must have been common in both marine and nonmarine habitats.

Like similar sized birds, such smaller pterosaurs as *Gallodactylus, Pterodactylus,* and *Rhamphorhynchus* are usually interpreted as having been capable of both efficient flapping and gliding (Wiman, 1923, 1925; Wellnhofer, 1970, 1975c, 1978; Fabre, 1976). Webbed hind feet have been postulated for *Pterodactylus* and *Rhamphorhynchus,* and the animals were probably able both to land on and take off from water (Wellnhofer, 1970, 1975b, c).

However, most authors (Lucas, 1902; Bramwell & Whitfield, 1970, 1974; Bramwell, 1971; Heptonstall, 1971, 1972; Whitfield & Bramwell, 1971; Whitfield, 1979; Brower, 1980; Langston, 1981) have thought that such large forms as *Pteranodon* were mostly gliders

and soarers with marginal ability for powered flight. Birds with similar habits include the albatross, frigate birds, condors, and large vultures. Stein (1975) proposed the contrary view that *Pteranodon* was a poor glider or soarer that was adapted for slow flapping flight, but Bramwell and Whitfield (1974) estimated that 68 watts of power were required for *Pteranodon* to fly level; they also calculated that the useful power output of the animal was only 78 watts. These data and somewhat similar figures given by Brower (1980) indicate that *Pteranodon* was minimally powered and more probably glided and soared. We believe that such other large taxa as *Nyctosaurus, Dsungaripterus,* and *Quetzalcoatlus* were also primarily gliders and soarers (see Brower, 1980).

Soaring has a considerable metabolic advantage over active flapping for a large animal because the power requirement is lower. For example, Baudinette and Schmidt-Nielsen (1974) measured various rates in herring gulls (average mass 0.91 kg) and found that the metabolic rate while gliding or soaring is about twice the basal or resting metabolic rate, whereas the metabolic rate during flapping flight equals approximately seven times the resting rate. Pennycuick (1972b) suggested that the fuel consumption rate for flapping flight in the white-backed vulture (mass 5.38 kg) is 30 times that for soaring. Based on the figures for wing area, body weight, and gliding performance calculated by Bramwell and Whitfield (1974) and by Brower (1980), *Pteranodon* was adapted for relatively low horizontal flying speeds in conjunction with slow sinking speeds (see McMasters, 1974 and Brower, 1980 for comparative data on *Pteranodon,* other organisms, and man-made gliders). The gliding performance of *Pteranodon* and probably other large pterosaurs was ideally suited to slope, thermal, and convection-current soaring in light winds.

Some of the small pterosaurs might have been insectivorous (Wellnhofer, 1970, 1975c, 1978; Langston, 1981), and the sievelike teeth of *Ctenochasma* and *Pterodaustro* could represent an adaptation to plankton feeding (Wellnhofer, 1975c), but fragments of fish and crustaceans have been found in the beak of *Pteranodon* (Brown, 1943). Many large pterosaurs, as well as most large-toothed species, were probably fish eaters (Brown, 1943; Bramwell & Whitfield, 1974). However, Lawson (1975a) noted that *Quetzalcoatlus northropi* apparently lived inland and might have scavenged carcasses of large dinosaurs. Langston (1981) suggested that the beak and long neck of this animal were probably an adaptation to probing of animal burrows.

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STATISTICAL METHOD

Allometry, defined as the study of change in shape as correlated with increase in size, may be applied to ontogenetic or phylogenetic sequences, or to a static series of mature organisms (Gould, 1966). This last type of allometry is the subject of this paper. Most of the allomet-

ric relationships analyzed here are bivariate, and the main statistics are derived from the simple power function or allometric equation, which has been discussed by Huxley (1932), White and Gould (1965), Gould (1966, 1971, 1977) and Brower and Veinus (1978). The equation is $Y = a \cdot X^b$, in which X and Y are the independent and dependent variables, respectively. The intercept a equals Y when X is unity. The possible biological significance of a has been subject to much debate (White & Gould, 1965; Gould, 1966, 1971, 1977). For this study, a is considered only as a location and scale parameter for the curve. The exponent b is the ratio of the specific rates of change in Y and X. For example, if the exponent is 0.0, then Y remains constant regardless of X. Where b is greater than 0.0, Y increases as X becomes larger; where b is negative, Y decreases as X becomes larger. The exponent also reveals the changes in the shape ratio of Y and X. If b exceeds 1, then Y increases more rapidly than X and the Y to X ratio is augmented with larger X values. If b is less than 1, then the Y to X ratio decreases as X becomes larger. Where b equals 1, the Y to X ratio remains constant, and the rate of increase of Y per unit increment of X is stabilized.

A series of exponents for isometric change, in which the shape of the animal remains the same at all sizes, is needed to provide a scale for comparison with the allometric exponents based on observed change. In developing these isometric exponents, an area is a function of a linear dimension squared and a volume or mass is a function of a linear dimension cubed. Thus, when Y and X are both linear dimensions, $b = 1/1$ or 1; when Y is an area and X a linear dimension, $b = 2/1$ or 2; when Y is a volume or mass and X a linear dimension, $b = 3/1$ or 3; when Y is a linear dimension and X a volume or mass, $b = 1/3$ or 0.33; when Y is an area and X a volume or mass, $b = 2/3$ or 0.67; and when Y is a volume or weight and X an area, $b = 3/2$ or 1.5. Some isometric exponents are greater than 1.0; others are less. For those larger than 1.0, the value of the Y to X ratio always increases in larger organisms. If the isometric exponent is less than 1.0, the Y to X ratio becomes smaller in larger animals. The ratio of Y to X is constant, regardless of size, only if the exponent is 1.0.

The relation between isometric and observed exponents is as follows. If the observed exponent exceeds the corresponding isometric value, the shape changes with positive allometry. If the observed exponent is less than the isometric figure, the animal exhibits negative allometry. An observed exponent can be tested for significance against an isometric value by a simple Student's t-test, in which Students t equals the observed minus the isometric exponent divided by the standard error of the exponent. Student's t is tested with $(N-2)$ degrees of freedom, where N is the number of specimens.

The reduced major axis algorithm was used to calculate most of the bivariate equations for several reasons. The allometric equation is descriptive because the exponent and the initial intercept are not biased by the choice of independent and dependent variables. This technique assumes that the error variances are proportional to the standard deviations of the variables, a reasonable assumption where one is concerned with variables of different orders of magnitude. Discussion of the reduced major axis algorithm and computational details were presented by Imbrie (1956), Hayami and Matsukuma (1970), and Kuhry and Marcus (1977). Predictions of various parameters were required for *Quetzalcoatlus northropi* and *Q.* sp., and we have computed these equations based on least squares methods (see Sokal & Rohlf, 1969, pp. 405-448).

MEASUREMENTS

The original data set is based on 27 pterosaurs, listed at the end of this section, which represent most of the common genera in the order. It was possible to calculate the mass for only 16 of the pterosaurs, and these animals make up the final data set; some of the important data are presented in Table 4. Representative pterosaurs are shown in Figure 1. Generally each species is represented by a single set of measurements, although several specimens of common species of *Pterodactylus* were measured to check the consistency of the data for that genus. Many complete specimens of the various German species of *Pterodactylus* and *Rhamphorhynchus* are known (Wellnhofer, 1970, 1975b), but most of these were not used because we did not want a data set dominated by the ontogeny of members of these two

genera. Adult forms are of interest here. Several juveniles were measured, however, to extend the size range of the data and to include animals with masses equivalent to those of small birds and bats. If growth sequences were available for more species, more juveniles would have been included in the data set. Most of the data were taken from published restorations. (See specimen list for sources of data.) These measurements have been checked against those obtained from actual specimens, and the restorations are clearly accurate enough for this study. A few relatively complete specimens have been restored by us, but we have generally refrained from putting the bits and pieces back together. All measurements are in grams and centimeters.

The best measure of the overall size of an organism is its mass. The masses of the 16 pterosaurs have been estimated using a simplified version of the geometric technique developed by Bramwell and Whitfield (1974) for *Pteranodon.* Bramwell and Whitfield (1974) and most other workers have assumed an overall or bulk density of 1.0 g/cm^3, but our computations are based on a density of 0.9 g/cm^3. This figure seems more reasonable because the density of a plucked bird is 0.9 g/cm^3 (Welty, 1962). Colbert (1962) also worked with a density of 0.9 g/cm^3, taken from living birds and reptiles, to estimate the mass of various dinosaurs. Any animal consists of a suite of tissues with different densities. In a fish, for example, the following densities are known: dry bone, 2.0 g/cm^3; muscle, 1.05 g/cm^3; cartilage, 1.1 g/cm^3; and fat, 0.9 g/cm^3 (Alexander, 1968). Using a single bulk density, however, is much the simpler procedure and sufficiently accurate for our purpose. The animal is divided into parts and the volume calculated for each part separately. The mass is the total volume multiplied by the bulk density of 0.9 g/cm^3. Volumes of the various parts are calculated as follows.

Skull.—The skull bones are assumed to be 1.0 mm thick in pterodactyloids (e.g., Eaton, 1910; Wellnhofer, 1970; Bramwell & Whitfield, 1974) and 1.5 mm thick in rhamphorhynchoids (Wellnhofer, 1975a, b, c). The beak is approximated by a hollow cone and the central part of the skull by a hollow cylinder. The form of the rear of the skull is simulated by an elliptical shell of rotation for most forms and by a crest for *Pteranodon* (Bramwell & Whitfield, 1974); it is assumed to contain a brain and associated soft parts, modeled as a sphere or ellipse of rotation.

Bones of the neck, leg, and wing.—All bones are cylindrical except for the distal phalanx of the wing, which is treated as a cone. The bones of the wing and leg are hollow or pneumatic as in birds, but the thicknesses of the bone walls are not definitely known for most forms (see Eaton, 1910 and Bramwell & Whitfield, 1974 for data on *Pteranodon* and Wellnhofer, 1970, 1975a, b, c for other pterodactyloids and rhamphorhynchoids). Therefore, we have determined the total volume of the bones and assumed an overall density of 0.9 g/cm^3. This is our most significant departure from the more elaborate method of Bramwell and Whitfield (1974). They had detailed data on the thicknesses of these bones in *Pteranodon,* which allowed the calculation of the volumes of solid bone, pneumatic spaces, and tissue.

Wing membrane.—The density used for the wing membrane is 0.9 g/cm^3 and its thickness is taken at 0.15 mm for large forms and 0.1 mm for small forms by analogy with the wing membrane of a bat (Bramwell & Whitfield, 1974). Mass of the wing membrane is not critical because it comprises only a small portion of the mass (roughly 1.5 percent for *Pteranodon).*

Body.—The body constitutes the heaviest part of the animal, and its density is assigned a value of 0.9 g/cm^3, which seems reasonable inasmuch as it included air sacs, soft parts, and bone (Bramwell & Whitfield, 1974). The total volume of body is pieced together from volumes of various solids depending on the pterosaur. These range from straight or tapering cylinders and cones with circular cross sections to tapering objects with elliptical or more complicated cross sections. The total mass is found by summing the parts. Because most of the total mass is concentrated in the body (52 percent for *Pteranodon),* we have adopted a conservative procedure and computed the mass only of taxa in which the body dimensions are certain.

It is difficult to assess the accuracy of our simplified geometrical technique. Like Heptonstall (1971), we have estimated the masses of ourselves and several cooperative colleagues and obtained results to about 90 percent ac-

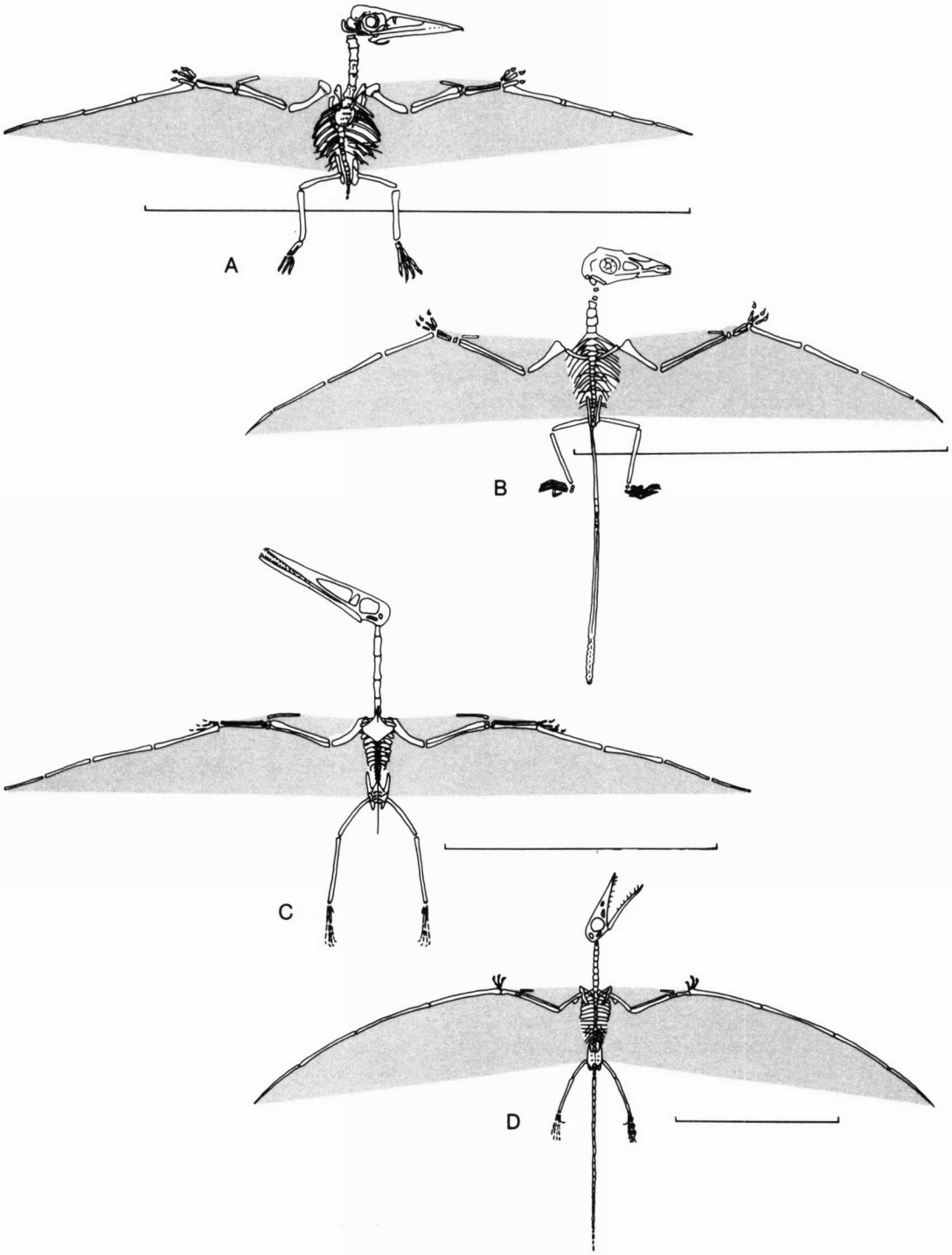


Fig. 1. Restorations of representative pterosaurs. Specimens are arranged in order of increasing mass. Scale bars are 20 cm. Wing membranes are shaded. Outlines of wing membranes are somewhat schematic; exact configurations near pteroid bone are not certain. Sources of data and selected measurements are listed under Measurements and in Table 4. Original drawings by Andi Kron of Los Alamos, New Mexico.——A. *Pterodactylus antiquus* (Soemmerring), young individual, study specimen 11.——B. *Sordes pilosus* Sharov, study specimen 4, configuration of wing membrane derived from Padian

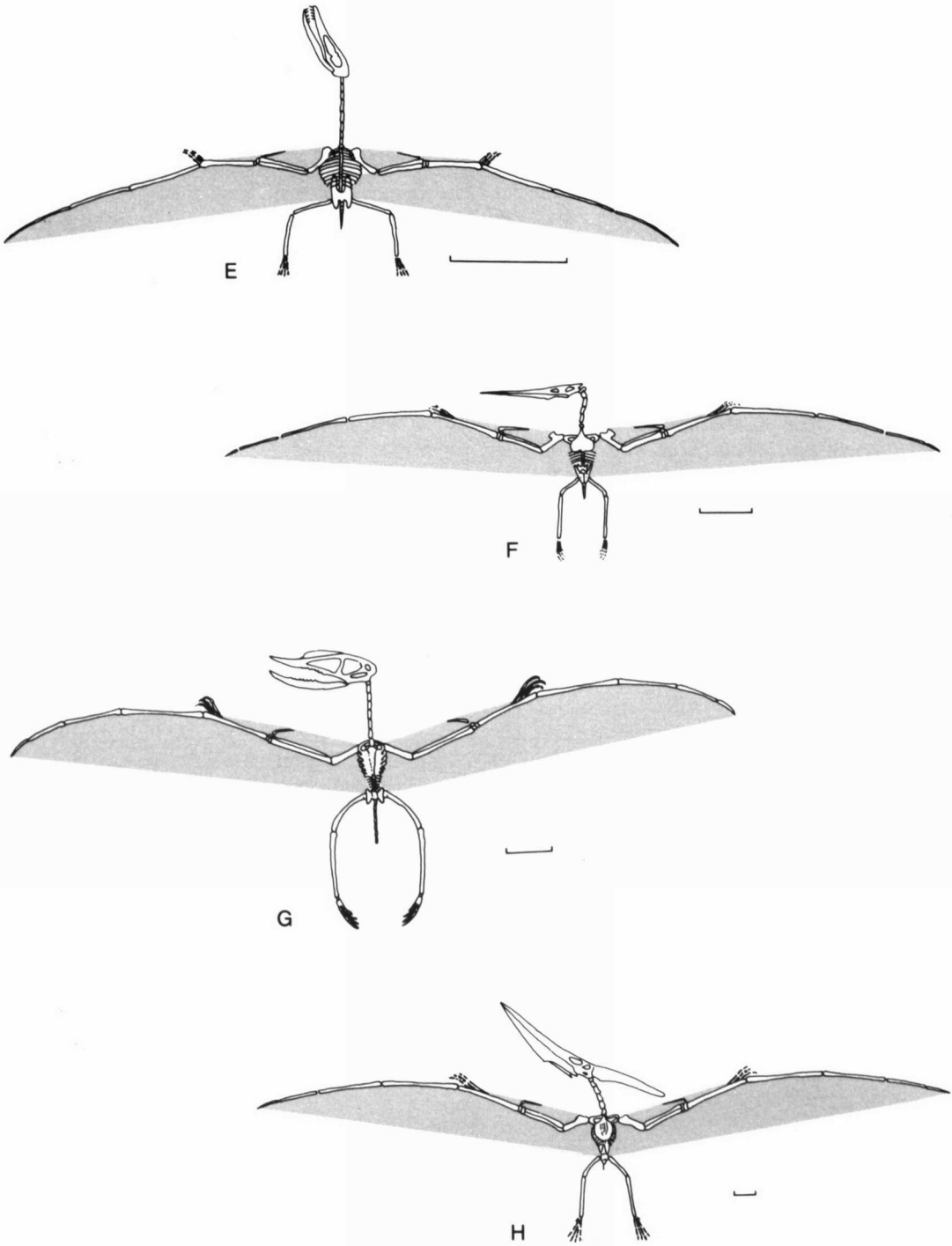


Fig. 1. Continued from preceding page.

(1979).——C. *Pterodactylus antiquus* (Soemmerring), mature animal, study specimen 12, redrawn.——D. *Rhamphorhynchus muensteri* (Goldfuss), study specimen 10, redrawn.——E. *Gallodactylus suevicus* (Quenstedt), study specimen 20, redrawn.——F. *Nyctosaurus gracilis* (Marsh), study specimen 25, redrawn.——G. *Dsungaripterus weii* Young, study specimen 23, restored.——H. *Pteranodon ingens* (Marsh), long-crested form, study specimen 27, redrawn.

curacy. Unfortunately, such checks are rather indirect. Our computations do agree with figures published by other workers, however. Bramwell and Whitfield (1974) tabulated masses of *Pteranodon* ranging from 12.9 to 29.8 kg with a middle value of 16.6 kg. Our calculated mass for *Pteranodon* is 14.94 kg. Most of the discrepancy between our figure and the middle value of Bramwell and Whitfield (1974) is caused by the difference in the assumed bulk density (0.9 and 1.0 g/cm^3). Various authors have produced similar computations for *Pteranodon* (11.3 kg by Williston, 1902; 30 kg by Kripp, 1943; 22.7 kg by Heptonstall, 1971; and 18.1 kg by Bramwell & Whitfield, 1970 and Bramwell, 1971); Stein (1975) postulated a mass of 15 kg by scaling up a bat. Based on careful anatomical study, Padian (1979) obtained a mass of 1.14 kg for *Dimorphodon macronyx;* our figure for the same animal is 1.07 kg. By analogy with birds, Watson (1974) suggested a mass of 200 g for a rhamphorhynchoid with a wingspan of 120 cm. Our calculated mass for *Rhamphorhynchus gemmingi* of roughly the same wingspan is 195 g. One would expect small birds and bats to weigh about the same as small pterosaurs. The smallest pterosaur has a wing area of 42.58 cm^2 and an estimated mass of 4.472 g. Based on equations listed by Greenewalt (1975b), small birds and bats of the same wing area have masses of 6.843 and 4.391 g, respectively. Our geometrical method has been employed to compute the mass of several small bats with an accuracy of about 90 percent. The similarity of all these figures is reassuring and indicates, at least to us, that our computations are reasonable and reliable.

The configuration of the pterosaur wing membrane is critical in the determination of wing area. The leading edge of the wing membrane was probably joined to the shoulder region (see Wellnhofer, 1970, 1975a, b, c). There is disagreement, however, about the trailing edge. Unlike many paleontologists, Padian (1979 and in preparation) outlined much evidence that the wing membrane was not attached to the hind legs, and this configuration is accepted here. The skeptical reader should examine the specimens of *Pterodactylus* and *Rhamphorhynchus* with preserved wing membranes and the restorations of these forms by Wellnhofer (1970, 1975a, b, c). These wing membranes are too short to reach the hind legs. The wing membrane is also preserved in *Sordes pilosus,* and Sharov (1971) pictured this animal with the wing membrane attached to the hind legs. Padian (1980, personal communication) suggested on the basis of photographs of the specimen that the wing membrane is folded over, and he judged that the wing membrane of *Sordes* could not have extended along the hind legs. To the best of our knowlege, wing membranes are not known for any other pterosaurs. We will assume that the basic design of the wing membrane was the same in all pterosaurs. The arrangement adopted here has the obvious advantage of freeing the hind legs for locomotion on the ground and in the water as in birds (see Fig. 1).

Frey and Riess (1981) have published a new reconstruction of the pterosaur wing in which the pteroid bone is roughly at a right angle to the wingspan. They believe that the leading edge of the wing membrane extended from the shoulder to the tip of the pteroid bone to parts of the fingers, and eventually joined the distal part of the wing finger. This configuration results in a much larger membrane along the leading edge of the wing than is visualized here (Fig. 1), and there are several strong arguments against it. Preserved wing membranes do not support their reconstruction (see Wellnhofer, 1970, 1975b, c, 1978; Padian, 1979); in fact, known wing membranes are most consistent with the arrangement used in this paper. According to Padian (June 1981, personal communication), the morphology of the pteroid bone indicates that it pointed toward the body. Padian also believes that the fingers are designed for grasping rather than supporting a membrane. Thus we consider that the wing membrane configurations herein are basically correct.

The arrangements of the wing bones were taken from various authors who have worked on the species involved (Wellnhofer, 1970, 1975a, b, c, on *Pterodactylus* and *Rhamphorhynchus;* Bramwell & Whitfield, 1974, on *Pteranodon;* Padian,1979, on *Dimorphodon).* The illustrations are reasonably general, and slightly different arrangements of the wing bones yield similar measurements of wingspan and wing area. Following standard aeronautical practice, the area of the wings includes the area of the body strip between wings (Simons,

1978). The wingspan or wingspread is the distance between wing tips. The aspect ratio was calculated by dividing the square of the wingspan by the area of the wings. All measurements of area were made with a digitizer.

In addition a series of standard linear dimensions have been determined. These comprise lengths of individual bones and various dimensions of the animals (Fig. 2). Not only the length but the diameter of the proximal shaft of the humerus, first phalanx of the wing, and femur were measured.

Pterosaur specimens and sources of data.— The numbers assigned below to specimens are the same as those used on the graphs in Figures 3, 4, 5, and 8.

Suborder Rhamphorhynchoidea Plieninger

1. *Dimorphodon macronyx* (Buckland). Jurassic, basal Lias, Sinemurian; Lyme Regis, Dorset, Eng. Owen, 1870, pl. 20.

2. *Anurognathus ammoni* Döderlein. U. Jurassic, Kimmeridgian, Malm Zeta 2; Solnhofen Ls., Ger. Wellnhofer, 1975b, Abb. 37; Müller, 1968, Abb. 430.

3. *Eudimorphodon ranzii* Zambelli. U. Triassic, up. Norian; Cene, Italy. Zambelli, 1973, figs. 1, 2; most measurements supplied by Dr. R. Wild.

4. *Sordes pilosus* Sharov. U. Jurassic, Russia. Sharov, 1971, pl. 1.

5. *Campylognathoides zitteli* (Plieninger). L. Jurassic, Toarcian, Ger. Plieninger, 1894, taf. 19.

6. *Scaphognathus crassirostris* (Goldfuss). U. Jurassic, Kimmeridgian, Malm Zeta 2; Solnhofen Ls., Ger. Wellnhofer, 1975b, Abb. 36.

7. *Dorygnathus banthensis* (Wagner). L. Jurassic, Toarcian; Holzmaden Beds, Ger. Wiman, 1923, pl. 1.

8. *Rhamphorhynchus gemmingi* von Meyer. U. Jurassic, Kimmeridgian, Malm Zeta 2; Solnhofen Ls., Ger. Wellnhofer, 1975c, taf. 30, fig. 1; Müller, 1968, Abb. 423a.

9. *R. longicaudus* (Münster). U. Jurassic, Kimmeridgian, Malm Zeta 2; Solnhofen Ls., Ger. Wellnhofer, 1976b, Abb. 22.

10. *R. muensteri* (Goldfuss). U. Jurassic, Kimmeridgian, Malm Zeta 2, Solnhofen Ls., Ger. Wellnhofer, 1975c, Abb. 41

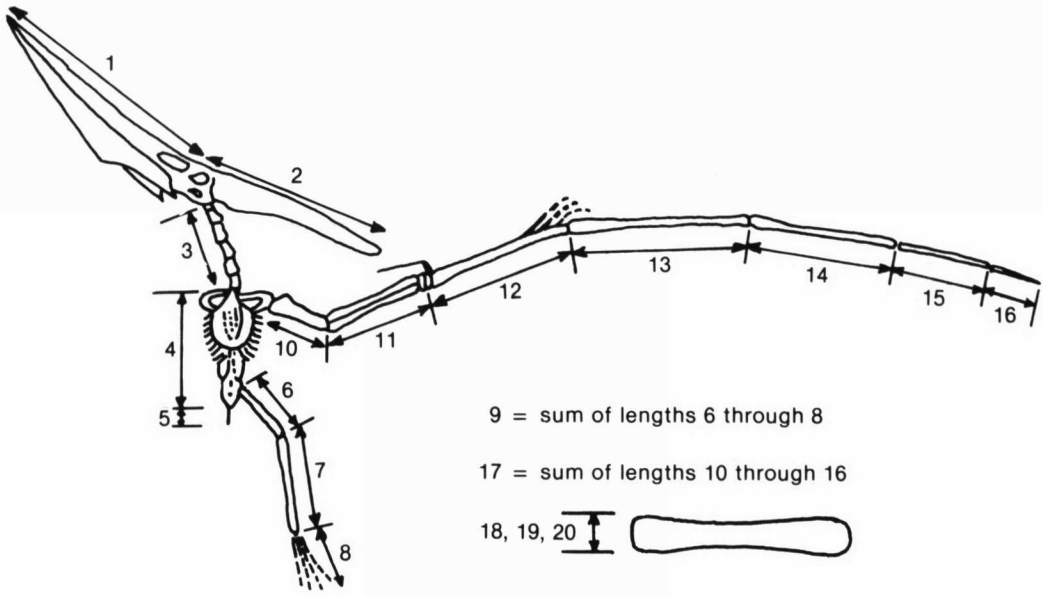


Fig. 2. Sketch of *Pteranodon ingens* showing measured features of study specimens. 1. Length of anterior part of head. 2. Length of posterior part of head. 3. Length of neck. 4. Length of body. 5. Length of tail. 6. Length of femur. 7. Length of tibia. 8. Length of foot. 9. Length of leg (sum of measurements 6-8). 10. Length of humerus. 11. Length of radius or ulna and one carpal. 12. Length of metacarpal and one carpal. 13, 14, 15, 16. Lengths of first, second, third, and fourth phalanges of wing, respectively. 17. Total length of wing bones (sum of measurements 10-16). 18, 19, 20. Greatest proximal diameter of humerus shaft, first phalanx of wing, and femur, in that order. All measurements in centimeters.

Suborder Pterodactyloidea Plieninger

11. *Pterodactylus antiquus* (Soemmerring). U. Jurassic, Kimmeridgian, Malm Zeta 2; Solnhofen Ls., Ger. Specimen originally described as *P. spectiabilis* von Meyer, see Wellnhofer 1970, p. 15 for synonomy; measured from cast in Syracuse University Collections; see fig. 360 in von Zittel, 1902.

12. *P. antiquus* (Soemmerring). Horizon as for specimen 11. Wellnhofer, 1970, Abb. 24.

13. *P. antiquus* (Soemmerring). Horizon as for specimen 11. Wellnhofer, 1970, taf. 1, fig. 1.

14. *P. elegans* Wagner. U. Jurassic, Kimmeridgian, Malm Zeta 2; Solnhofen Ls., Ger. Wellnhofer, 1970, taf. 8, fig. 1; von Zittel, 1902, fig. 359.

15. *P. kochi* (Wagner). U. Jurassic, Kimmeridgian, Malm Zeta 1-3; "Papierschiefer" and Mörnscheimer Sl., Ger. Specimen originally described as *P. scolapacieps* von Meyer; see Wellnhofer, 1970, p. 22, 23 for synonymy; Wiman, 1925, fig. 12; Müller, 1968, Abb. 426.

16. *P. kochi* (Wagner). Horizon as for specimen 15. Müller, 1968, Abb. 427.

17. *P. micronyx* von Meyer. U. Jurassic, Kimmeridgian, Malm Zeta 2; Solnhofen Ls., Ger. Specimen listed as *Ptenodracon brevirostris* by Seeley, 1901, fig. 59; see Wellnhofer, 1970, p. 36, 37 for synonymy; figured in Wellnhofer, 1970, Abb. 9.

18. *Gallodactylus canjuersensis* Fabre. U. Jurassic, Kimmeridgian; Gisement de Canjuers, Fr. Fabre, 1976, pl. 1, 2, fig. 2, 5.

19. *G. longicollum* (von Meyer). U. Jurassic, Kimmeridgian, Malm Zeta 1; Schieferkalke, Ger. Specimen listed as *Cycnorhamphus fraasi* by Seeley, 1901, fig. 63; see Wellnhofer, 1970, p. 57 for synonymy.

20. *G. suevicus* (Quenstedt). U. Jurassic, Kimmeridgian, Malm Zeta 1 and 2; Schieferkalke and Solnhofen Ls., Ger. Specimen listed by Seeley, 1901, fig. 60, 62, as *Cycnorhamphus suevicus;* see Wellnhofer, 1970, p. 55 for synonymy.

21. *Ctenochasma gracile* Oppel. U. Jurassic, Kimmeridgian, Malm Zeta 2; Solnhofen Ls., Ger. Brioli, 1936, fig. 1, pl. 1.

22. *Pterodaustro guinazui* Bonaparte. U. Jurassic or L. Cretaceous; low. mbr. Lagarcito Fm., Arg. Sanchez, 1973, pl. 1.

23. *Dsungaripterus weii* Young. L. Cretaceous; Sinkiang, China. Young, 1964, pl. 1.

24. *Nyctosaurus bonneri* Miller. U. Cretaceous; Niobrara Ls., Kans. Miller, 1971, p. 12, pl. 6, inadvertently listed it as *Pteranodon (Nyctosaurus) gracilis* on the plate legend.

25. *N. gracilis* (Marsh). U. Cretaceous; Niobrara Ls., Kans. Williston, 1902, p. 299.

26. *Pteranodon ingens* (Marsh), short-crested form. U. Cretaceous; Niobrara Ls., Kans. Williston, 1897, pl. 2; Lucas, 1902, pl. 1.

27. *P. ingens* (Marsh), long-crested form. U. Cretaceous; Niobrara Ls., Kans. Eaton, 1910.

ALLOMETRY OF BONES

ALLOMETRY OF BONE DIAMETER

For all measured bones, Table 1 lists the coefficients for the allometric equations as well as such statistics as the correlation coefficients, standard error of the slopes, and dispersion about the reduced major axis. The bones measured and representative pterosaurs are pictured in Figures 1 and 2.

As expected, the maximum diameter of the shafts of wing and leg bones show positive allometry, increasing rapidly in the larger pterosaurs. The larger forms are characterized by humeri, femora, and first phalanges of the wing finger that have thicker shafts relative to body size than do smaller forms (Fig. 1). This is also demonstrated by the bivariate equations (Table 1) which are roughly: (Maximum diameter of bone shaft) $\cong$ (Mass)$^{0.42}$.

Here the isometric exponent equals 0.33. (X is a mass and Y a linear dimension.) The observed exponent shows that the diameter of the bones is augmented more rapidly than expected based on isometric geometry, although the Student's t-values are not statistically significant. Translating the above linear data into the approximate areas, which will scale as the square of the diameter, the equation becomes: (Area of bone shaft) $\cong$ (Mass)$^{0.84}$. The isometric exponent for this relationship equals 0.67.

The positive allometry of bone diameter is definitely a response to the problems of support, both in the wing and leg. That the ob-

Table 1. *Allometric Equations for Bone Dimension and Mass for 16 Pterosaurs.* (Independent variable mass for all equations; computed by reduced major axis algorithm; measurements in grams and centimeters; Student's *t*-test compares observed with isometric exponent, 0.33.)

Dimension and bone	*a*	Exponent	Correlation coefficient	Standard error	Student's *t*-value	Dispersion about axis	*N*
Proximal shaft diameter							
Humerus	0.07799	0.4040	0.9080	0.04231	1.669	0.4922	16
First phalange	0.06205	0.4247	0.9051	0.04515	2.024	0.5036	16
Femur	0.04307	0.4394	0.8740	0.05338	1.987	0.5834	16
Length							
Body	1.702	0.3412	0.9797	0.01710	0.4581	0.2265	16
Leg	2.456	0.3722	0.9739	0.02112	1.839	0.2594	16
Femur	0.6682	0.3852	0.9571	0.02790	1.857	0.3340	16
Tibia	0.9752	0.3915	0.9734	0.02243	2.596[a]	0.2636	16
Foot	0.7742	0.3394	0.9653	0.02216	0.2729	0.2960	16
Anterior part of head	1.414	0.4254	0.9760	0.02316	3.974[a]	0.2533	16
Posterior part of head	0.03110	0.6519	0.8180	0.09370	3.400[a]	0.7659	16
Neck	0.9661	0.4163	0.9325	0.03758	2.206[a]	0.4235	16
Tail (rhamphorhynchoid)	5.093	0.3372	0.9492	0.05305	0.07289	0.1910	4
Tail (pterodactyloid)	0.3397	0.4030	0.9317	0.04414	1.578	0.4517	11
Humerus	0.7279	0.3528	0.9850	0.01522	1.280	0.1954	16
Radius and ulna	1.110	0.3582	0.9885	0.01354	1.835	0.1714	16
First phalange	1.033	0.4316	0.9526	0.03282	2.993[a]	0.3568	16
Second phalange	1.056	0.4089	0.9716	0.02419	3.125[a]	0.2740	16
Third phalange	0.8789	0.3952	0.9695	0.02422	2.555[a]	0.2826	16
Fourth phalange	0.8974	0.3323	0.9326	0.02999	−0.03343	0.4117	16
Metacarpal (rhamphorhynchoid)	0.4939	0.2977	0.9981	0.008269	−4.309[a]	0.0467	5
Metacarpal (pterodactyloid)	0.7264	0.4619	0.9923	0.01729	7.436[a]	0.1553	11
Bones in one wing	6.351	0.3935	0.9844	0.01731	3.478[a]	0.2020	16

[a]Student's *t*-value significant at 0.05 risk level.

served exponent is less than 1.0 indicates the support ratio (i.e., area of bone shaft divided by mass) decreases in progressively larger pterosaurs. However, the observed rate of decline of the support ratio is less than if the change were isometric. Similar changes are known in ontogenetic and phylogenetic change of vertebrates ranging from the smallest shrews to giant dinosaurs like *Diplodocus*. Two well-known examples are the ontogeny of the domestic chicken (Cock, 1963) and the evolution of pelycosaurs (Gould, 1967). In fact, the presence of relatively thicker bones in progressively larger animals was first described by Galileo in 1638.

Such positive allometry was perhaps critical for large pterosaurs. The safety factor for a particular structure equals its breaking strength or load divided by the forces applied to the structure during flight. Bramwell and Whitfield (1974) and Heptonstall (1971) calculated the strength of the humerus in *Pteranodon*. Bramwell and Whitfield (1974) estimate the safety factor of this pterosaur bone at about 2.0, whereas most birds have safety factors of about 4.0. This strength estimate for the pterosaur is based only on bone and does not include the strengthening effects of muscles, tendons, air sacs, etc. Nevertheless *Pteranodon* seems minimally stressed compared to birds, although rather violent maneuvers are required to exceed a safety factor of 2.0. On the basis of our data, one would expect the safety factor of a pterosaur significantly larger than *Pteranodon* to be less than 2.0.

The initial intercepts also contain pertinent information. The exponents of the equations for all three bones are almost the same, but the initial intercepts differ, with that of the humerus being largest and that of the femur being smallest (Table 1). The rate of increase in diameter of the bone shaft is most pronounced in the humerus and least so in the femur. It is notable that the diameter of the bones is augmented more rapidly in the wing than in the leg of larger pterosaurs.

ALLOMETRY IN THE LEGS, BODY, NECK, AND HEAD

For all practical purposes, the body length is isometric with respect to mass. The allometric equation (Table 1, Fig. 3A) is: (Body length) = 1.64 (Mass)$^{0.341}$, and this seems quite reasonable inasmuch as the body ranges from 40 to 55 percent of the total mass in most of the pterosaurs studied.

The legs show slight positive allometry compared to mass but negative allometry relative to wing length (Table 1, Fig. 3B). The allometric equations are: (Length of leg) = 2.46 (Mass)$^{0.372}$ and (Length of leg) = 0.428 (Length of wing)$^{0.946}$. Thus the legs of larger pterosaurs are slightly longer compared to mass but smaller in relation to the wing, a change that has been noted by many authors (see Fig. 1). This change is found mostly in the tibia and to a lesser extent in the femur. Length of the foot exhibits isometry with respect to body size. Apparently once a foot is large enough to walk on, paddle with, grasp, or groom the animal, it need not become proportionally larger (see Wellnhofer, 1970, 1975c and Bramwell & Whitfield, 1974 for discussion of the functions of pterosaur feet).

Scaling of the head is complex. The lengths of both the anterior and posterior parts of the head, especially the latter, are characterized by strong positive allometry with respect to size (Fig. 3C). The allometric equations are: (Length of anterior part of head) = 1.41 (Mass)$^{0.425}$, and (Length of posterior part of head) = 0.031 (Mass)$^{0.652}$.

For the posterior part of the skull, this positive allometry is largely caused by the crest in the large form, *Pteranodon ingens*. However, in other large forms the rear of the head extends proportionally farther back than in smaller species (Fig. 1).

The purpose of the crest of *Pteranodon* has aroused much speculation, which was reviewed by Bramwell and Whitfield (1974) and Stein (1975). The main postulated functions are: as ornamentation; as an aid in weight saving (it counterbalanced the anterior part of the head,

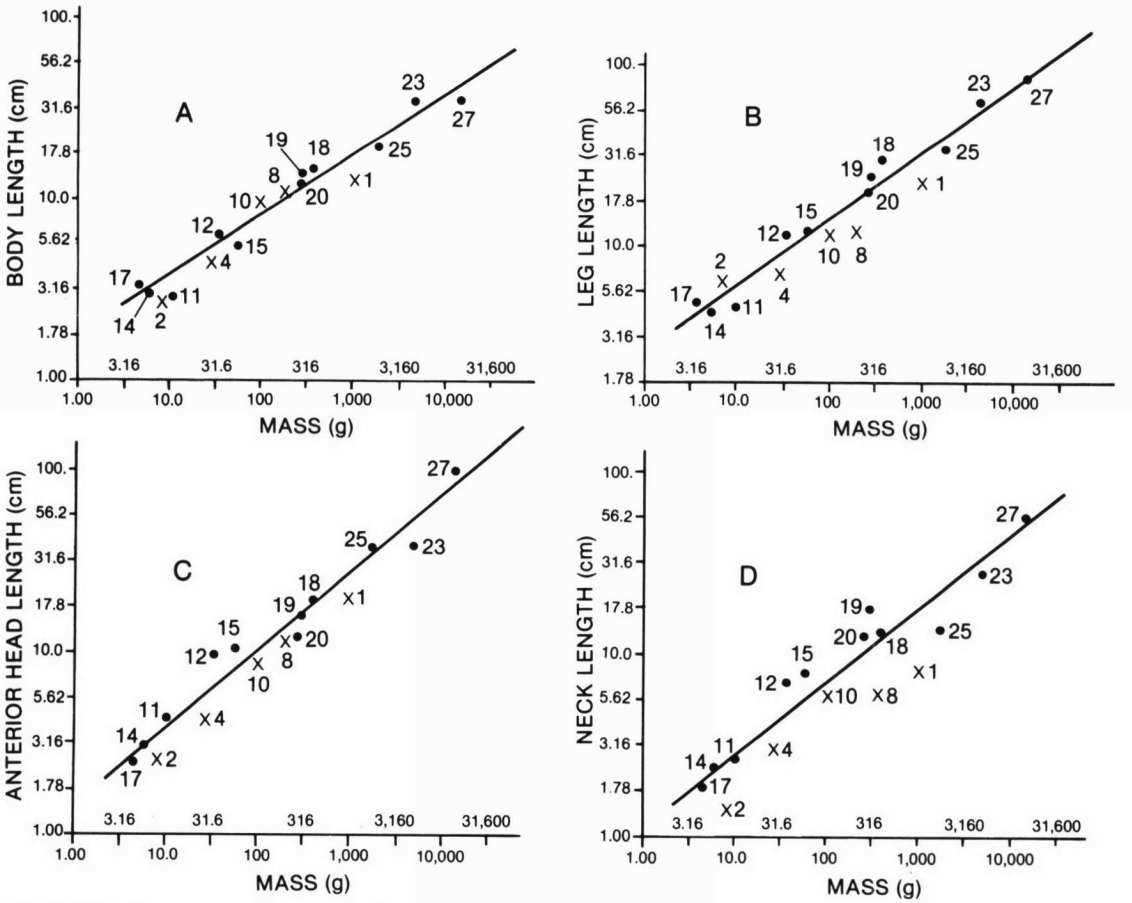


Fig. 3. Plots of mass versus linear dimensions for 16 pterosaurs: A, body length; B, leg length; C, anterior head length; D, neck length. Study specimen numbers correspond to those in Measurements. Dots indicate pterodactyloids; crosses, rhamphorhynchoids.

allowing reduction of the neck muscles); as an area for attachment of muscles used in raising the head and closing the jaws; as an airbrake; and as a forward rudder or centrally mounted steering device (designs that work in model airplanes if the device is large enough). Regardless of the function of the crest of *P. ingens,* a crest was clearly not critical to all large pterosaurs (Short, 1914), for some lack them (*Nyctosaurus;* see Fig. 1).

Like that of the skull, the allometry of the neck is positive versus body size (Fig. 3D), in which the relation is: (Length of neck) = 0.966 $(\text{Mass})^{0.416}$. Thus in larger pterosaurs generally compared to the smaller ones, the head is definitely larger and slightly more slender with longer jaws and a bigger posterior area capping a somewhat elongate neck. The largest forms, *Pteranodon* and *Nyctosaurus,* are also toothless (Fig. 1).

Many of the transformations in the head and neck can be tied to feeding habits and to weight reduction. Loss of teeth and thinning of bones in the head (the thickness of blotting paper in *Pteranodon* according to Eaton, 1910) must have resulted in a considerable saving of mass. Because such pterosaurs as *Dimorphodon, Dorygnathus, Eudimorphodon, Pteranodon, Rhamphorhynchus,* and at least some species of *Pterodactylus* were clearly fish eaters —fish scales, etc. are commonly preserved in the jaws and rib cages of specimens of these taxa (Brown, 1943; Wellnhofer, 1970, 1975c, 1978; Bramwell & Whitfield, 1974; Wild, 1978)—and crustaceans have been recorded from the jaw of *Pteranodon* (Brown, 1943), their possible fishing strategies are of interest. Some seabirds fly just above the waves and dip or skim the water for food, others land in the water and seize fish on and just under the surface, still others plunge or dive (see Ashmole, 1971; Dorst, 1974). The fragile construction of pterosaurs, especially the larger forms, argues against plunging, and the shape of the animals does not seem designed for diving although this might have been possible. Unlike water-skimming birds, pterosaurs have the lower and upper jaws the same length. Thus we believe that most pterosaurs were dippers or seizers of fish. Due to the problems of takeoff from water by large flying animals, *Pteranodon* and most other large pterosaurs are generally visualized as fish-eaters that flew over the waves in search of small fish and crustaceans, scooping them up in the beak, storing the food in either a throat pouch or the stomach, and eventually returning to the shore to digest food and feed their young without having to land in the water (Bramwell & Whitfield, 1974; Stein, 1975). The increased length of the head and neck can probably be associated with these habits. Such morphological changes would have allowed fishing with little or no danger of an unexpected dunking, an obvious hazard for a large flying beast with a wingspread of 6.9 m or more. If large pterosaurs landed on the water, a long head and neck would have permitted the seizing of prey over a larger radius. According to Lawson (1975a), the landlocked Texas pterosaur *Quetzalcoatlus northropi* probably ate carrion, the remains of large dinosaurs, a habit in which the benefits of long jaws and neck seem obvious. Langston (1981) believed that the beak and long neck of this species were an adaptation to probing burrows made by various organisms. At any rate, elongated jaws and necks offer at least some degree of adaptive versatility.

Rhamphorhynchoids have shorter heads and necks than pterodactyloids of the same mass (Fig. 3C, D). This fact could be related to differences in posture between the two suborders; the Pterodactyloidea were birdlike, whereas the Rhamphorhynchoidea were similar to small bipedal dinosaurs (Padian, 1980, personal communication).

SIZE AND SHAPE OF THE TAIL

The longer tails of the Rhamphorhynchoidea distinguish them from the Pterodactyloidea (Figs. 1, 4). The equations for the two groups are: (Tail length of pterodactyloids) = 0.340 $(\text{Mass})^{0.403}$, and (Tail length of rhamphorhynchoids) = 5.09 $(\text{Mass})^{0.337}$. Tail and mass change in the rhamphorhynchoids is isometric; however, the exponent of the pterodactyloids is somewhat greater than the isometric figure of 0.33. The generally longer tail of rhamphorhynchoids is reflected by the initial intercept, which is much larger than for the pterodactyloids.

The diagnostic morphologic features of rhamphorhynchoids and pterodactyloids suggest considerable phylogenetic divergence and perhaps different adaptations. (We presume pterosaurs are monophyletic.)

The long tail of rhamphorhynchoids is generally thought to be a stabilizing device (see Bramwell & Whitfield, 1974; Wellnhofer, 1975c). Forms such as *Rhamphorhynchus* have a vane at the end of the tail (Wellnhofer, 1975c). However, a tail vane is apparently lacking in at least one rhamphorhynchoid, *Sordes*. Although poorly preserved, the wing membrane of this form is partially known, and there is no trace of a tail membrane although the posterior extremity of the tail is somewhat flattened (Sharov, 1971); it seems reasonable to expect that the wing and tail membranes would both have been preserved if they were present. When present, the tail vane was oriented vertically and it doubtless functioned as a moveable rudder (Marsh, 1882; Wellnhofer, 1975c). Padian (1980 personal communcation) reported that the articulation of the tail bones and the associated soft parts show that the tail vane could not have served as a horizontal stabilizer. Bramwell and Whitfield (1974) postulated that the long tail of rhamphorhynchoids also could have provided inertial control during flight. If relatively rigid, the tail could function in the same way as a tight-rope walker's pole. If it were like the highly flexible tail of a monkey, it would allow much more sophisticated inertial control. The orientation of the tail in many specimens of pterosaurs shows that most of the tail was moderately stiff and that most movement was confined to its base (Ostrom, 1969; Wellnhofer, 1975c). This would definitely limit the use of the tail in inertial control to aiding balance in flight and on the ground. The shorter tail of pterodactyloids is consistent with less inherent stability, and these animals may have been more maneuverable. (Bramwell & Whitfield, 1974; Stein, 1975); such adaptation to flight is well known in bats (Vaughan, 1970a, b). Most authors consider the Rhamphorhynchoidea as phylogenetically the more primitive of the two suborders (for example, Saint-Seine, 1955; Wellnhofer, 1978). If so, pterosaurs have followed the path toward flight adopted in most flying organisms and man-made flying devices, in which stable flyers evolve into less stable and more maneuverable configurations (Maynard-Smith, 1952).

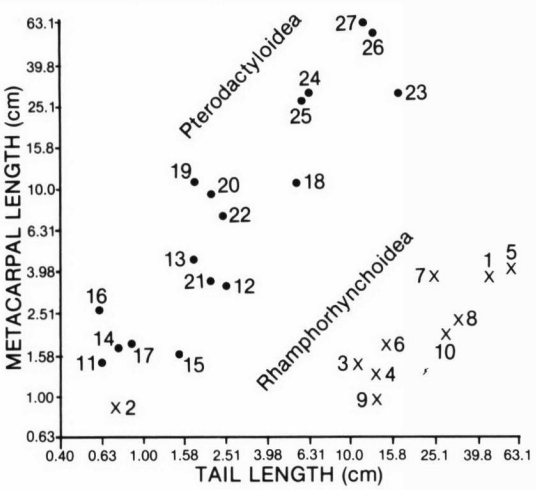


Fig. 4. Plot of tail length versus metacarpal length for 27 pterosaurs. Study specimen numbers are as in Measurements. Dots indicate pterodactyloids; crosses rhamphorhynchoids.

According to Padian (1980 personal communication), the contrasts in tail length between the Rhamphorhynchoidea and Pterodactyloidea are closely correlated with the differences in posture mentioned in discussion of head and neck features.

SIZE AND SHAPE OF THE WING BONES

As in birds, the wing becomes longer relative to body size in progressively larger pterosaurs. A distinct Huxleyan gradient of allometry is present in the wing, in which various parts change at different rates; and the entire wing is a mosaic of differential patterns of size and shape changes. The gradient represents an adaptation with the following features. The smallest exponents for length of wing bones are those for the humerus, radius and ulna, and the fourth or distal phalanx; the Student's *t*-values denote that these observed exponents do not differ significantly from the isometric values of 0.33 (Table 1). Thus, the slowest rates of increase occur in bones at the proximal and distal extremities of the wing. Two of the applicable equations are: (Length of humerus) = 0.728 $(Mass)^{0.353}$, and (Length of fourth phalanx) = 0.897 $(Mass)^{0.332}$. These minimum rates of increase could have adaptive significance. A relatively shorter, thicker humerus, radius, and ulna might be related to the mechanics of support. During flight, these bones must have borne all the loads generated; as noted previously, the forces or loads of powered flight exceed those for level gliding or soaring (Heptonstall, 1971; Bramwell & Whitfield, 1974). The shorter fourth or distal

phalanx may have minimized the possibility of flexing of the wing tip during turning, banking, or flapping. Stein (personal communication 1976) pointed out that a shorter distal phalanx would have been particularly useful for powered flight because it would have been better able to sustain the high wing-tip loads produced by flapping.

The most rapid increase of length in the wing bones of larger animals is found in the three proximal phalanges of all forms and in the metacarpal of the pterodactyloids (Table 1). The Student's t-values indicate that the observed exponents are significantly larger than isometric values. The rates of increase become smaller in the more distal phalanges. Two of the equations are: (Length of proximal or first phalanx) = 1.03 $(\text{Mass})^{0.432}$, and (Length of second phalanx) = 1.06 $(\text{Mass})^{0.409}$.

The allometry of the metacarpal of the two suborders is strikingly different. As discussed before, the rhamphorhynchoid metacarpal is short in comparison to that of the pterodactyloids (Figs. 1, 4). The allometric equations are: (Metacarpal length of Rhamphorhynchoidea) = 0.494 $(\text{Mass})^{0.298}$ and (Metacarpal length of Pterodactyloidea) = 0.726 $(\text{Mass})^{0.462}$. The longer metacarpal of pterodactyloids is reflected by initial intercepts and exponents that are larger than those of the rhamphorhynchoids. Positive allometry exists for the Pterodactyloidea, but Rhamphorhynchoidea exhibit negative allometry.

One of the major features of pterosaurs is positive allometry of the total length of all wing bones with respect to mass (Table 1), with the allometric equation: (Length of all wing bones) = 6.35 $(\text{Mass})^{0.393}$. This pattern is also seen in birds, but not in bats, a phenomenon that is discussed in subsequent parts of this paper.

ALLOMETRY OF MASS, WINGSPAN, AND ASPECT RATIO

The wingspan of pterosaurs is positively allometric relative to mass (Fig. 5A; Table 2). The equation is: (Wingspan) = 12.2 $(\text{Mass})^{0.401}$. The large Student's t-value shows that the observed exponent is significantly higher than the isometric figure of 0.33. Larger pterosaurs have wings that are longer compared to mass than do smaller taxa (Fig. 1). The comparative figures used below for the birds are approximate because they were derived from other equations given by Greenewalt (1975b). We fitted the bat equation to Greenewalt's (1962) data. The bird and bat equations are: (Wingspan) = 7.76 $(\text{Mass})^{0.412}$ ("passeriform" birds of Greenewalt, 1975b), and (Wingspan) = 11.6 $(\text{Mass})^{0.324}$ (bats). Like the pterosaurs, birds exhibit positive allometry for wingspan in relation to mass, but the initial intercept of the bird equation is much lower than that of the pterosaurs because pterosaurs possess longer wings than birds of the same mass. Unlike pterosaur wingspan, that of bats is isometric with respect to mass.

The aspect ratio, which is the square of wingspan divided by wing area, provides an important measure of wing shape and aerodynamic performance (Lighthill, 1975, 1977; Simons, 1978). High aspect ratios typically denote long, thin wings whereas short, stout wings have lower aspect ratios. The equation for the 16 pterosaurs (Table 2, Fig. 5B) is: (Aspect ratio) = 7.90 $(\text{Mass})^{0.102}$. As in birds (Greenewalt, 1975b), the aspect ratio is generally augmented with increasing mass and wingspan, although the data are widely scattered. The aspect ratio is a dimensionless parameter. Such isometric flyers as bats exhibit constant aspect ratios; the isometric exponent for an equation of aspect ratio versus mass is 0.0. The large Student's t-value shows that the exponent of the pterosaurs is significantly greater than nil. The change of aspect ratio is largely a function of wingspan and the body length (see Fig. 1). As just mentioned, the wingspan exhibits positive allometry relative to mass; also, the body becomes shorter with respect to the wingspan in progressively larger pterosaurs.

The scaling of the aspect ratio is important aerodynamically because it controls induced drag. (Induced drag, which is sometimes called vortex drag, is caused by the production of lift. See Dommasch, Sherby, & Connolly, 1961; Alexander, 1968; Pennycuick, 1972a; and Simons, 1978 for discussion of induced drag in airplanes and organisms.) This type of drag is inversely proportional to the aspect ratio:

$$C_{Di} = \frac{kC_l^2}{\pi \mathcal{R}},$$

in which C_{Di} is the induced drag coefficient, k is

a constant which is taken at 1.1 here (Bramwell & Whitfield, 1974), C_l is the coefficient of lift, and $\mathcal{R}$ is the aspect ratio. The equation shows that larger pterosaurs with their higher aspect ratios generate less induced drag relative to their size than smaller forms do.

MASS AND WING AREA

The relationship of wing area and mass is obviously important for any flyer because the wing must be large enough to support the mass during flight. The equation for mass and wing area of the 16 pterosaurs is: $(\text{Mass}) = 0.0408\ (\text{Wing area})^{1.27}$ (see also Table 2; Figs. 5C, 6). (A note on units is required. The equations were computed in grams and square centimeters; for some parts of this paper, these units have been translated into kilograms and square meters in order to quote smaller numbers.) If one wishes to consider wing area as a function of mass, the equation is: $(\text{Wing area}) = 12.4\ (\text{Mass})^{0.788}$.

In the first equation, the exponent is much less than the isometric value of 1.5. In the second equation, the observed exponent exceeds the isometric value of 0.67. The large Student's *t*-values (Table 2) denote that the differences are statistically significant at a probability level of much less than 0.001. Thus, mass is subject to strong negative allometry relative to wing area; that is, weight increases much more slowly than for isometric flyers. It is perhaps more appropriate to visualize the situation in reverse: that wing area is positively allometric relative to mass. Algebraically, the two statements are equivalent, and statistically we cannot choose between hypotheses. Biologically the two hypotheses are not the same. If the data consisted of an ontogenetic sequence of one species, one might be able to select in favor of one or the other possibility. However, for our static series of adults, we are content to give both formulations and leave selection to the reader. Padian (1980 personal communication) thinks in terms of positive allometry of wing area with respect to mass. Nevertheless, we will discuss mass as a function of wing area because this convention was employed by Greenewalt (1975b) in his tabulations on insects, birds, and

Table 2. *Allometric Equations for the Wing in Relation to Mass for Pterosaurs and Other Flyers.* (Data for pterosaurs, hang-gliders, and bats computed by reduced major axis algorithms; Greenewalt (1975b) equations fitted by a technique yielding similar results. Measurements in grams, centimeters, square centimeters and grams per square centimeters; Student's *t*-test compares observed with isometric exponent.)

Flyer	*X*	*Y*	*a*	Exponent	Correlation coefficient	Standard error	Isometric exponent	Student's t-value	Dispersion about axis	*N*
Pterosaurs	Mass	Wingspan	12.24	0.4014	0.9870	0.01610	0.33	4.231[c]	0.1786	16
"Passeriform" birds[a]	"	"	7.764	0.4122	-----	------	0.33	------	-----	555
"Shorebirds"[a]	"	"	7.150	0.4033	-----	------	0.33	------	-----	138
Bats[b]	"	"	11.63	0.3240	0.9690	0.02138	0.33	−0.4365	0.1593	14
Pterosaurs	Wingspan	Mass	0.001951	2.491	0.9870	0.09990	3.0	−5.093[c]	0.1786	16
	Mass	Aspect ratio	7.9012	0.1017	0.07891	0.02534	0.0	4.012[c]	1.405	16
	Wing area	Mass	0.04077	1.270	0.9958	0.02908	1.5	−7.926[c]	0.1203	16
"Passeriform" birds[a]	"	"	0.05935	1.266	0.9855	0.00913	1.5	−25.63[c]	-----	555
"Shorebirds"[a]	"	"	0.04425	1.400	0.9865	0.0200	1.5	−5.000[c]	-----	138
"Ducks"[a]	"	"	0.08210	1.400	0.9688	0.0523	1.5	−1.912	-----	46
Bats[b]	"	"	0.01442	1.524	0.9589	0.1200	1.5	0.2000	-----	15
Hang-gliders	"	"	0.001121	1.508	0.9817	0.02887	1.5	0.2771	0.1191	99
Pterosaurs	Mass	Wing area	12.43	0.7877	0.9958	0.01804	0.67	6.706[c]	0.1203	16
Pterosaurs	Mass	Wing loading	0.07472	0.2274	0.9483	0.01804	0.33	−5.871[c]	0.3398	16
"Passeriform" birds[a]	"	" "	0.1074	0.2099	-----	------	0.33	------	-----	555
"Shorebirds"[a]	"	" "	0.1078	0.2857	-----	------	0.33	------	-----	138
"Ducks"[a]	"	" "	0.1677	0.2857	-----	------	0.33	------	-----	46
Bats[b]	"	" "	0.05231	0.4021	0.9081	0.04500	0.33	1.528	0.2815	14
Hang-gliders	"	" "	0.007527	0.3713	0.9404	0.01269	0.33	2.992[c]	0.1911	99

[a]Greenewalt, 1975b.
[b]Greenewalt, 1962.
[c]Student's *t*-value significant at 0.05 risk level.

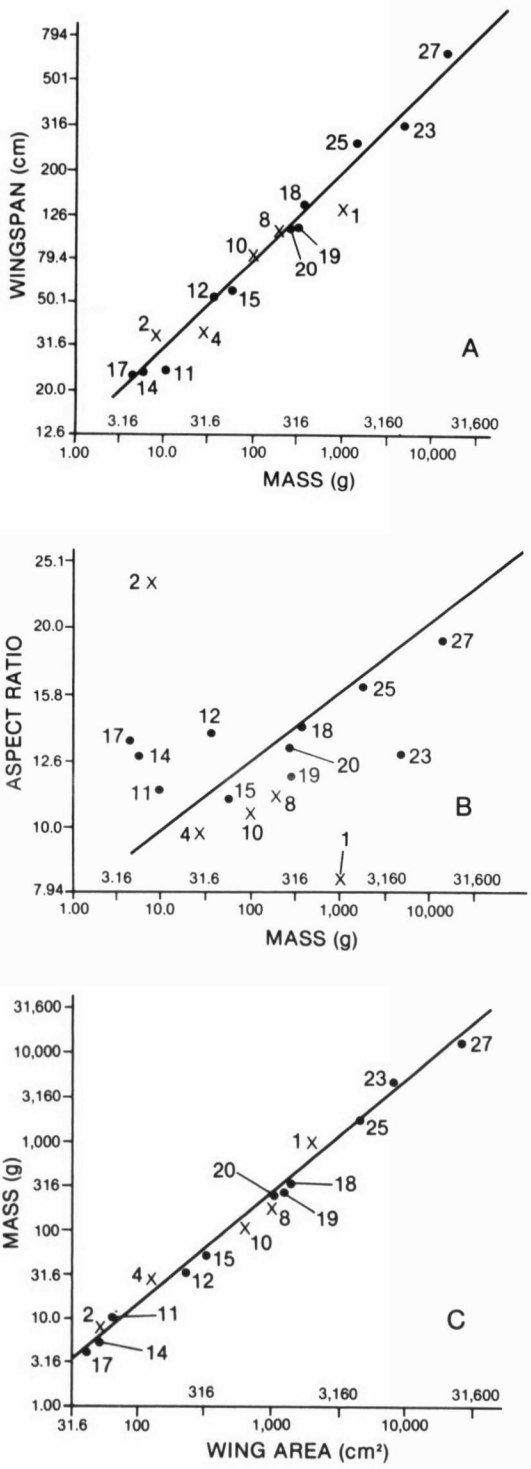


Fig. 5. Plots of mass versus A, wingspan; B, aspect ratio; C, wing area, for 16 pterosaurs. Study specimen numbers are listed in Measurements. Dots indicate pterodactyloids; crosses rhamphorhynchoids.

bats. For the pterosaurs, the ratio of mass to wing area increases only from about 0.10 g/cm² in the smallest animal to 0.59 g/cm² in *Pteranodon ingens,* obviously in response to the problem of flight by progressively larger animals. Within the limits of the basic geometry, this increase of wing area relative to mass keeps wing loadings (mass divided by wing area) and flight speeds within reasonable bounds, as discussed later. Some of the main morphological features of this allometry are discussed below.

Bones.—It seems likely that at least some bones of all or most pterosaurs were pneumatic (Wellnhofer, 1970, 1975a, b, c, 1978; Bramwell & Whitfield, 1974), and the largest pterosaurs developed bones with very thin walls in the wing and skull. For example, in *Pteranodon,* the best known large form, many of the walls are less than 1.0 mm thick (Eaton, 1910; Bramwell & Whitfield, 1974). Although data are not available for all taxa, the bone walls almost certainly became thinner with respect to the overall size of the bones in larger pterosaurs. In bones of the wing finger, the ratio of bone wall thickness to average diameter of bone is 0.27 in *Pterodactylus antiquus* (Wellnhofer, 1970, pl. 4, fig. 5), 0.15 in *Rhamphorhynchus muensteri* (Wellnhofer, 1975a, text-fig. 15a), and only 0.049 in *Pteranodon ingens* (Bramwell & Whitfield, 1974, fig. 2).

Body and leg length.—The most obvious change is increase of the wing area relative to the linear dimensions of the body, an important feature because about half of the mass is in the body. The decrease in the size of the legs in comparison to the wing is also significant. The proportions of the legs relative to the body, however, remain roughly the same regardless of mass (see previous equations).

Teeth.—Teeth are relatively dense skeletal elements. It is noteworthy that the teeth are lost in all large pterosaurs except *Dsungaripterus* and *Ornithodesmus.* In these forms, the teeth are relatively small and are restricted to roughly half of the jaw (Wellnhofer, 1978, p. 5-10).

One of the end results of these trends, *Pteranodon* with a wingspread of 6.95 m, has a wing loading of 0.59 g/cm², a figure much lower than wing loadings in such large soaring birds as *Gyps africanus* (white-backed vulture) and *Diomedea exulans* (an albatross), with 0.78 and 1.37 g/cm², respectively.

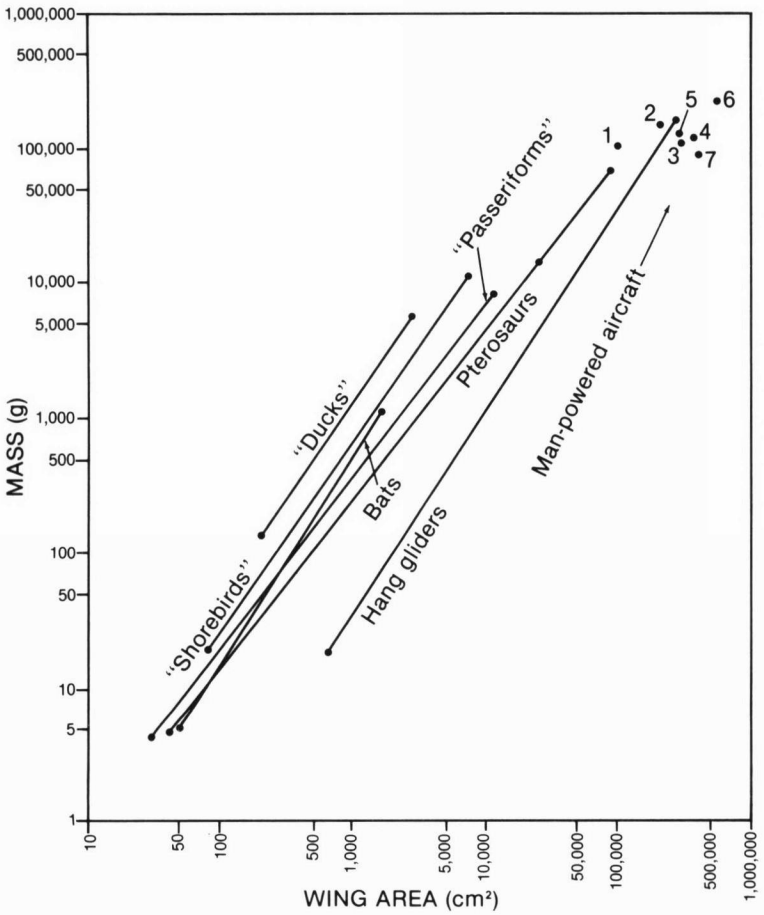


Fig. 6. Plot of equations of mass versus wing area for the various flyers. The numbered points are for man-powered aircraft (data from Sherwin, 1975). 1. Mufli. 2. Pedaliante. 3. SUMPAC. 4. Puffin II. 5. Jupiter. 6. Toucan I. 7. Gossamer Albatross.

The relative mass and wing area of birds, bats, and pterosaurs is an intriguing question. Greenewalt (1975b; see 1962 for original data) published equations for these parameters in several groups of flying animals. A brief explanation of Greenewalt's aerodynamic grouping of birds is necessary. The "passeriforms" include such diverse birds as cranes, eagles, frigate birds, gulls, hawks, herons, owls, some petrels, shearwaters, terns, and vultures in addition to the expected families. The albatross, bustards, curlews, gannets, most geese, parrots, plovers, sandpipers, snipes and swans are regarded as "shorebirds." Most of the birds that might be ecologically similar to pterosaurs fall into one of these two groups. The "duck" group is relatively coherent, containing ducks, grebes, loons, coots, and the Canada goose. Although the groups of birds established by Greenewalt have no taxonomic meaning, they are useful aerodynamically. These groups are based mainly on wing loading (mass divided by wing area). Most of the birds with low wing loadings are assigned to the "passeriforms"; those with the highest wing loadings are placed in the "duck" group. Intermediate wing loadings are generally observed in "shorebirds." The aerodynamic importance of wing loadings will be discussed later, but Greenewalt's bird groups have been accepted by most aerodynamists working on flying animals (see Lighthill, 1977; Rayner, 1979). Throughout the text we will employ Greenewalt's names for bird groups in quotation marks. Greenewalt (1962, 1975b) aside, various other workers also tabulated data on the wing area and mass of bats, but their information has not been used because the data are dominated by small bats. Greenewalt (1962, 1975b) also assembled information on several groups of insects. These data will not be discussed here, for insects are not in the same size range as pterosaurs. Moreover, the wings of

insects and of pterosaurs are neither homologous nor are they constructed in the same fashion. The equations for bats and the various groups of birds are listed below with the equation previously derived for pterosaurs (see Table 2; Fig. 6, and the sketches of the wings in Fig. 7).

$$(\text{Mass}) = 0.0144\,(\text{Wing area})^{1.52}\ (\text{bats})$$
$$(\text{Mass}) = 0.0594\,(\text{Wing area})^{1.266}\ (\text{"passeriforms"})$$
$$(\text{Mass}) = 0.0442\,(\text{Wing area})^{1.4}\ (\text{"shorebirds"})$$
$$(\text{Mass}) = 0.0821\,(\text{Wing area})^{1.4}\ (\text{"ducks"})$$
$$(\text{Mass}) = 0.0408\,(\text{Wing area})^{1.27}\ (\text{pterosaurs})$$

The allometric relationships are graphed in Figure 6, and their relative positions should be noted. The lines for pterosaurs and the "passeriforms" have by far the smallest exponents, 1.270 and 1.266, versus 1.4 to 1.52 for the other groups. Thus the pterosaurs and the "passeriforms" show the most negative allometry of mass relative to wing area of all flyers studied. The other animals are either isometric or are subject to less negative allometry. Almost identical exponents are observed for pterosaurs and "passeriform" birds. However the much smaller initial intercept of the pterosaurs locates the pterosaur line in a region of larger wing areas for the same mass. The exponents for the "shorebirds" and the "ducks" exceed that of the pterosaurs, and the wing areas of "shorebirds" and "ducks" are smaller than those of pterosaurs of equivalent mass.

The initial part of the pterosaur data intersects that of the bats, but most of the pterosaur line is displaced above those for the other organisms on the plot of wing area versus mass. Therefore, middle-sized and large pterosaurs have larger wing areas than would bats of the same mass. The overlap between data points for pterosaurs, bats, and many of the birds will be discussed in the next section. It is important to realize that pterosaurs and the "passeriform" birds reached the largest sizes of any of the flying animals. For example *Pteranodon,* the largest well-known pterosaur, has a mass of 14.9 kg and the calculated mass of *Quetzalcoatlus northropi* is about 75 kg. The mass of the largest flying bird, a Tertiary teratorn from Argentina, has been estimated at about 80 kg (Campbell, personal communication, Feb. 1981; see also Campbell 1980; Anonymous, 1980). This animal belongs to the "passeriform" group of Greenewalt (1975b). The largest "ducks" and "shorebirds" weigh from about 6 to 13 kg (Greenewalt, 1962, 1975b). According to McFarland and others (1979), the mass of the largest bat is 1.6 kg.

McMasters (1976; see Fig. 7) pointed out that the wings of pterosaurs are structurally analogous to Rogallo-wing hang-gliders with high aspect-ratio wings (see later discussion). Rogallo-wing hang-gliders do not have wing ribs although battens are present in some types, and the single leading-edge spar usually consists of aluminum tubing. The wing membrane or sail is made of Dacron or some similar material. The wing membrane is attached to the leading-edge spar and also to an axial spar or keel in the center of the glider. Markowski (1977) provided a useful review of hang-gliders. Similarly, Stein (1975) has drawn analogy between the pterosaur wing and the sail of a boat. The Princeton Sailwing and Sailvanes are also similar; here, a rigid leading edge and a flexible wing membrane are present, but the trailing edge is made from a tensioned wire (see Fink, 1967, 1969; Strong, 1974; Maughmer, 1979).

We compiled data for 92 full-size Rogallo-wing hang-gliders and four Princeton Sailwings from Price (1975); the figures for the mass include an average-sized pilot. The wing area and weight were also determined for three flying-model Rogallo-wings: the 1/16 scale model made by Entex Industries Inc., the Drachenflieger kite and glider sold in the USA by F.A.O. Schwartz, and the 1/6 size radio-controlled Flexiflier constructed by Kelly (1974). Inasmuch as static models do not glide, these were not measured. The largest and smallest wingspreads (11.8 m and 43.6 cm), wing areas (26.7 m^2 and 648 cm^2), and masses (139 kg and 20.4 gm) show that the size range of hang-gliders is reasonably comparable to that of pterosaurs. The hang-glider equation (Table 2, Fig. 6) is: $(\text{Mass}) = 0.00112\,(\text{Wing area})^{1.51}$. Hang-gliders, then, are nearly isometric, but the extremely small initial intercept was puzzling until we realized that the models were built to scale rather than designed for optimal flight performance. Although the masses of the largest pterosaur and full-sized hang-gliders with their pilots are roughly the same, most of the gliders have larger wing areas. Moreover, the hang-glider equation is simply not applicable to small pterosaurs. If the wing area of the smallest pterosaur (42.58

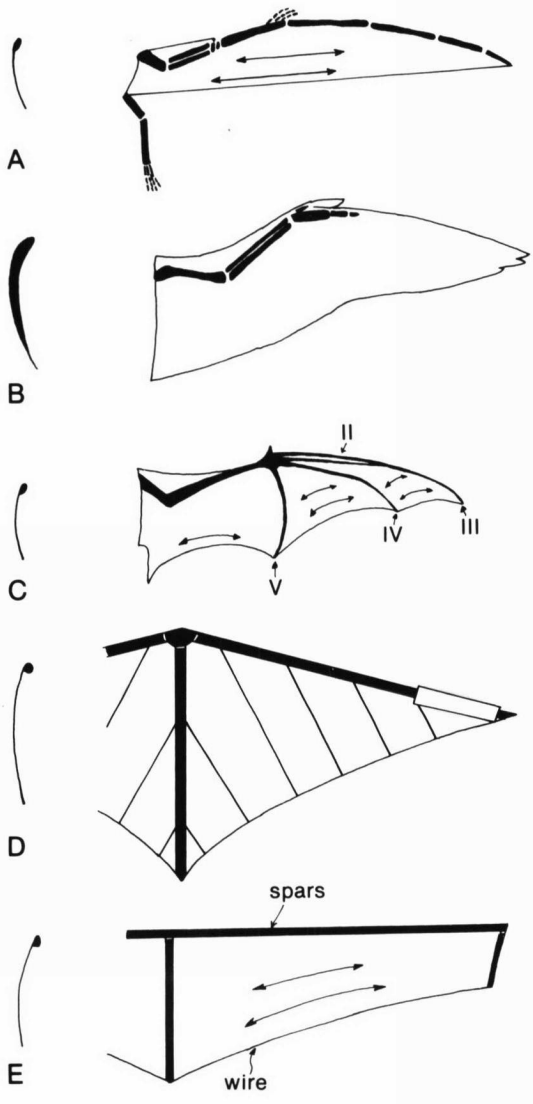


Fig. 7. Wing design and airfoils of various flyers. The wing spars or bones are drawn in heavy black. The arrows illustrate the main direction of tensioning of the wing membranes in A, C, and E. The trailing edge of the wing membranes of D and E are curved because these bow up in flight to form the airfoil. All airfoils are schematic.——A. Pterosaur, *Pteranodon ingens*.——B. Bird with high aspect-ratio wing, herring gull, *Larus argentatus*.——C. Bat with high aspect-ratio wing, *Eumops perotis* (Vaughan, 1970a, b). The Roman numerals indicate the different digits of the hand.——D. High-performance Rogallo-wing hang-glider, Cronkite V (after Price, 1975). This is the largest known hang-glider, with a wingspan of about 11.8 m.——E. Hang-glider wing of Princeton Sailwing type, Sailvane 2 (after Price, 1975; Maughmer, 1979). The trailing edge of the wing is tensioned with a wire.

cm²) is substituted into the hang-glider data, the calculated mass is only 0.321 g, perhaps a reasonable value for a feather or an insect but not for a pterosaur.

The data for seven man-powered aircraft are also given on Figure 6 (points 1-7, data from Sherwin, 1975). The oldest man-powered aircraft is "Mufli," which lies close to the largest pterosaur (point 1). The later and more sophisticated man-powered aircraft lie below the pterosaur line because of their larger wing areas with respect to mass (points 2-7). In general, the man-powered aircraft cluster close to the hang-gliders. The Gossamer Albatross (point 7), the most successful man-powered aircraft to date, was recently pedaled across the English Channel; this craft exhibits the lowest mass relative to wing area of all of the flyers in its size range.

MASS AND WING LOADING

Two definitions are commonly given in the aeronautical literature for the wing loading: mass divided by wing area or weight divided by wing area. The former is used here; units of computation are g/cm². The information given by a relationship between mass and wing loading is the same as that of mass versus wing area, but differently expressed. Aeronautical engineers usually treat relationships between mass and wing area in terms of wing loading because such aspects of flight performance as horizontal speed, etc. are either directly dictated by or closely correlated with wing loading (see later discussion). The equation for the 16 pterosaurs (Table 2, Fig. 8) is: (Wing loading) = 0.07472 $(\text{Mass})^{0.2274}$.

The isometric exponent, 0.33, greatly exceeds the observed figure. Obviously, pterosaurs represent a population in which the wing loading was subject to striking negative allometry. As indicated by the small initial intercept and exponent, the wing loading begins low and is augmented rather slowly in the larger pterosaurs. The lowest wing loading, 0.10 g/cm², occurred in the smallest pterosaur (mass 4.47 g). One of the end results of this process, *Pteranodon* (mass 14.9 kg), has a wing loading of only 0.59 g/cm², much lower than those of such large soaring birds as the Andean condor and the albatross, with wing loadings of 1.04 and 1.37 g/cm². The estimated wing loading of *Quetzalcoatlus northropi* (mass 75 kg) is only

0.89 g/cm² (see later discussion). The observed exponent is also close to zero, which would be the case if wing loading were constant regardless of mass.

The equations for the other flying organisms as well as the data points for man-powered aircraft are graphed in Figure 9 (Table 2). For the bird groups, the data were calculated from the equations of mass versus wing area published by Greenewalt (1975b), and so some of the statistical parameters (for example, standard error of slope) are not available. The equations are:

$$\text{(Wing loading)} = 0.05231\ (\text{Mass})^{0.4021}\ \text{(bats)}$$
$$\text{(Wing loading)} = 0.1074\ (\text{Mass})^{0.2099}\ \text{(“passeriforms”)}$$
$$\text{(Wing loading)} = 0.1078\ (\text{Mass})^{0.2857}\ \text{(“shorebirds”)}$$
$$\text{(Wing loading)} = 0.1677\ (\text{Mass})^{0.2857}\ \text{(“ducks”)}$$
$$\text{(Wing loading)} = 0.007527\ (\text{Mass})^{0.3713}\ \text{(hang-gliders)}$$
$$\text{(Wing loading)} = 0.07472\ (\text{Mass})^{0.2274}\ \text{(pterosaurs)}$$

The exponents in the equations for pterosaurs and “passeriform” birds are the smallest by a wide margin; these groups exhibit the most marked negative allometry of all the flyers, and their wing loadings are augmented more slowly with increasing size and mass than those of other groups. Less negative allometry is observed for this relationship in “shorebirds” and “ducks” than in “passeriforms” and pterosaurs. The hang-gliders and bats are either almost isometric or show slight positive allometry of wing loading relative to mass.

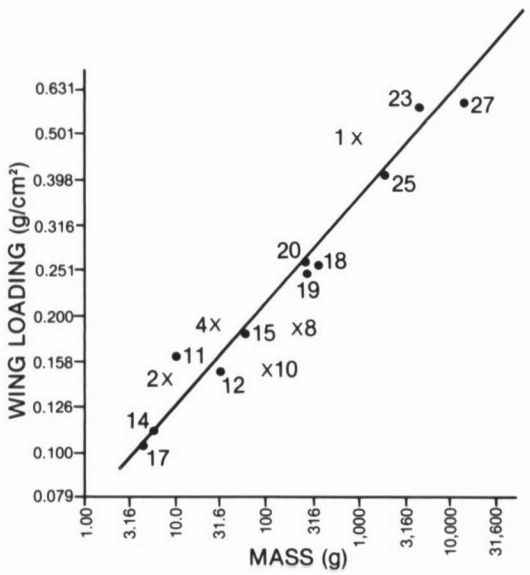


Fig. 8. Plot of mass versus wing loading for 16 pterosaurs. Study specimen numbers are given in Measurements. Dots indicate pterodactyloids; crosses, rhamphorhynchoids.

The position of the data for the pterosaurs relative to the other flyers in Figure 9 and Figure 10 is critical, and it suggests some analogies for flight performance. Initial parts of the curves of mass versus wing loading for bats and pterosaurs overlap, and wing loadings in small bats and small pterosaurs are similar. The equations diverge with larger masses, and bigger bats show much higher wing loadings than do pterosaurs of the same mass (Fig. 10C). Although their wing designs are quite different in most other respects (see Fig. 7 and Vaughan, 1970a, b for discussion of wing design and flight in bats), bats and pterosaurs both have membranous wings. These similarities imply that the flight performances of the two groups share some common features.

Small and medium-sized birds that exhibit active flapping flight typically have wing loadings that exceed those of pterosaurs of the same mass (Figs. 10A, B, D-F). However, the wing loadings of such small birds as swifts, swallows, small falcons, hawks, gulls, and terns intergrade with those of pterosaurs (Fig. 10D-F). In addition, these birds possess high aspect-ratio wings somewhat similar in outline to those of the small pterosaurs. These similarities of wing loading and aspect-ratio suggest that there may be some parallel features of flying habits here also. However, the feathered wing surfaces and airfoils of birds are less like those of a pterosaur than are bat wings (Fig. 7; see Kaufmann, 1970, Lighthill 1975, 1977, and Pennycuick, 1975 for readable accounts of flight of birds). The aerodynamics of bird wings are probably quite different from those of pterosaurs. The primary feathers of birds can be used as individual propellers (see Kaufmann, 1970; Kokshaysky, 1977). Vinogradov (1951, cited in Rayner, 1979) believed that birds can create suction flow through the wing. Neither of these alternatives is possible in pterosaurs or bats. Nevertheless, study of the plots of wing loadings versus mass suggests some very general conclusions.

Although a variety of flying habits is represented, all of the birds and bats that overlap with pterosaurs are efficient flappers with plenty of power reserves, and the same was almost certainly true of small pterosaurs. Unfortunately, the aerodynamic data do not conclusively point to any particular flight style for

small pterosaurs. Slightly larger pterosaurs (mass from about 150 to 300 g) fit with larger terns and some seagulls, buzzards, and hawks (Figs. 10E, F). These birds are either active flappers or they do both flapping and gliding or soaring.

The mass of pterosaurs such as *Nyctosaurus* and *Pteranodon* varied from about 1.86 to 14.9 kg with wing loadings from 0.41 to 0.59 g/cm². Such pterosaurs are generally considered to have been soarers and gliders (Bramwell & Whitfield, 1974; Wellnhofer, 1978), and some of the smaller pterosaurs may also have had the same mode of life (Wellnhofer, 1970, 1975c). The wing loadings of soaring sea and land birds generally exceed those of pterosaurs with the same mass (Figs. 10E, F), although some overlap exists. For example, some of the lightly loaded hawks and vultures plot with or close to the pterosaurs in the interval from about 300 g to 10 kg. So do some sea birds: several kinds of gull, terns, petrels, and frigate birds. (Strangely enough, the wing loadings of some owls are roughly the same as those of pterosaurs of the same mass, although there are doubtless few, if any, ecological similarities between the two groups; see Fig. 10B.) It is notable that the wings of pterosaurs are more similar in planform (shape in plan view) to the high aspect-ratio wings of sea birds such as the albatross, frigate birds, and many gulls than to the lower aspect-ratio wings of most hawks, owls, and vultures. At any rate, we believe that it should be possible to extrapolate cautiously from soaring sea and land birds with low wing loadings to pterosaurs in the range of masses from approximately 0.5 to 15 kg.

Wing loading for hang-gliders is lower than for pterosaurs of the same mass (Fig. 9). Hang-gliders are almost isometric for mass versus wing loading, and the initial portion of the hang-glider equation is not applicable to pterosaurs, because the wing loadings of small pterosaurs greatly exceed those of the small model hang-gliders. The largest pterosaur, *Quetzalcoatlus northropi,* has an estimated mass of about 75 kg, which corresponds to a wing loading of 0.89 g/cm². The mass of a typical hang-glider, including an average-sized pilot, equals about 100 to 120 kg. Although not apparent from the plot of the equations in Figure 9, the wing loadings of full-size Rogallo-wings are somewhat variable, ranging from 0.37 to 0.89 g/cm² (Price, 1975; Markowski, 1977). In general, the higher wing loadings, roughly 0.70 to 0.89 g/cm², are observed in the Rogallo-wings with large aspect-ratios and the best gliding performance. The largest and smallest wing loadings for the four Princeton sailwings, which are also high-performance hang-gliders, are 0.70 and 0.94 g/cm² (Fink, 1967, 1969; Price, 1975; Markowski, 1977; Maughmer, 1979). These figures are close enough to those of the largest pterosaur so that, as postulated by McMasters (1976), the high-performance hang-gliders may provide useful insights into the flight of the largest pterosaurs. We realize that the hang-glider analogy is quite general

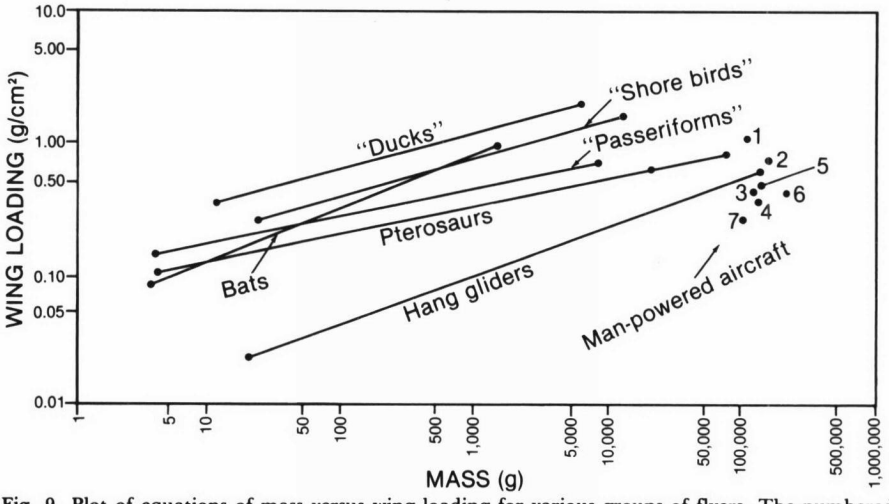


Fig. 9. Plot of equations of mass versus wing loading for various groups of flyers. The numbered points are for man-powered aircraft (data from Sherwin, 1975). 1. Mufli. 2. Pedaliante. 3. SUMPAC. 4. Puffin II. 5. Jupiter. 6. Toucan I. 7. Gossamer Albatross.

because flying organisms are dynamically unstable whereas man-made flying devices such as hang-gliders and model airplanes have more inherent stability. The flying models of *Pteranodon* constructed by Bramwell and Whitfield (see Whitfield, 1979) and *Rhamphorhynchus* made by von Holst (1957) provide classic examples of this. The model *Pteranodon* required a reflexed airfoil along with a fin and rudder to glide in a stable fashion (Whitfield, 1979). The flapping model *Rhamphorhynchus* was stabilized by using the tail vane as a horizontal stabilizer as in most model ornithopters. However, the tail vane of pterosaurs was oriented vertically according to Wellnhofer (1975c), and it could not have functioned as a stabilizer during flight. In addition, pterosaurs obviously possessed mechanisms of control that hang-gliders do not have. Pterosaurs could vary the planform and camber of one or both wings during flight as do birds and bats. (See Hankin & Watson, 1914; Short, 1914; Kaufmann, 1970; Vaughan, 1970a, b; Bramwell, 1971; Bramwell & Whitfield, 1974; Lighthill, 1975, 1977; Pennycuick, 1975 for discussions of control in flying animals.) During flapping flight, birds, bats, and presumably also pterosaurs often change the power stroke of one or both wings during turning and banking. Most hang-glider pilots steer their aircraft by shifting the center of gravity with respect to the center of lift and by warping the wing spars to change the angle of attack of various parts of the wing (see Markowski, 1977). The directions of wing movement that are postulated for pterosaurs indicate that the animals could exert this type of control also (Bramwell & Whitfield, 1974).

The man-powered aircraft are also noteworthy. The earliest of these aircraft, Mufli (Fig. 9, point 1), has a wing loading almost equal to that of the largest pterosaur and higher than that of most hang-gliders. The highly successful Gossamer Albatross exhibits a very low wing loading relative to pterosaurs and hang-gliders of the same mass (point 7). Other man-powered aircraft have slightly lower wing loadings than typical hang-gliders in the same weight range.

SIZE OF THE TEXAS PTEROSAURS

A lively debate has developed about the size of *Quetzalcoatlus northropi,* the giant pterosaur from Texas (Greenewalt, 1975a; Lawson, 1975a, b; McMasters, 1976; Stein, 1976). According to Lawson (1975a), *Q. northropi* is closely related to *Pterodactylus antiquus* from the Solenhofen Limestone of Germany (see Wellnhofer, 1970 for taxonomy). Lawson (1975a) suggested that, based on a humerus length of 52 cm, the wingspan of the animal was between 11 m and 21 m, although he preferred a value of 15.5 m. Drawing on analogies with birds, Greenewalt (1975a) calculated a wingspan of only 5.25 m. McMasters (1976) favored a wingspan of about 11 m for *Quetzalcoatlus northropi* because of the problems of control experienced in large Rogallo-wing hang-gliders. Lawson (1975b) reiterated his belief in a large wingspan and published a series of equations for wingspan versus humerus length which yielded the following predicted wingspans for the Texas animal: the *Pterodactylus antiquus* equation, 8.981 m; the *Pteranodon* equation, 12.08 m; the equation derived from Greenewalt's data, 5.239 m; and the approximate regression equation, 16.17 m. Note that these are only approximate wingspans because they are derived from the sum of the bone lengths in each wing; actual wingspans will be slightly less (see Fig. 1). We fitted least-squares equations for these parameters to several sets of data and obtained the following estimated wingspans for *Quetzalcoatlus northropi:* from our data on all pterosaurs, 14.08 m; from data on *Pterodactylus kochi* (Wellnhofer, 1970), 10.86 m; and from data on *P. micronyx* (Wellnhofer, 1970), 25.81 m.

Various species of pterosaurs show quite different patterns of allometry for wingspan relative to humerus length. Furthermore, the allometric equation for all pterosaurs diverges greatly from that for any one species. As implied earlier, the allometry of these parameters in mature specimens of the two suborders, the Rhamphorhynchoidea and Pterodactyloidea, is not significantly different. These data suggest that one cannot predict the wingspan of *Quetzalcoatlus northropi* by extrapolating the relationships seen in other groups of pterosaurs. Langston (1980 personal communication, see also 1981) is studying the Texas material, and he reports that the wingspan of *Quetzalcoatlus northropi* is probably between 10.67 and 12.19 m; a value of 11.43 m will be assumed for our

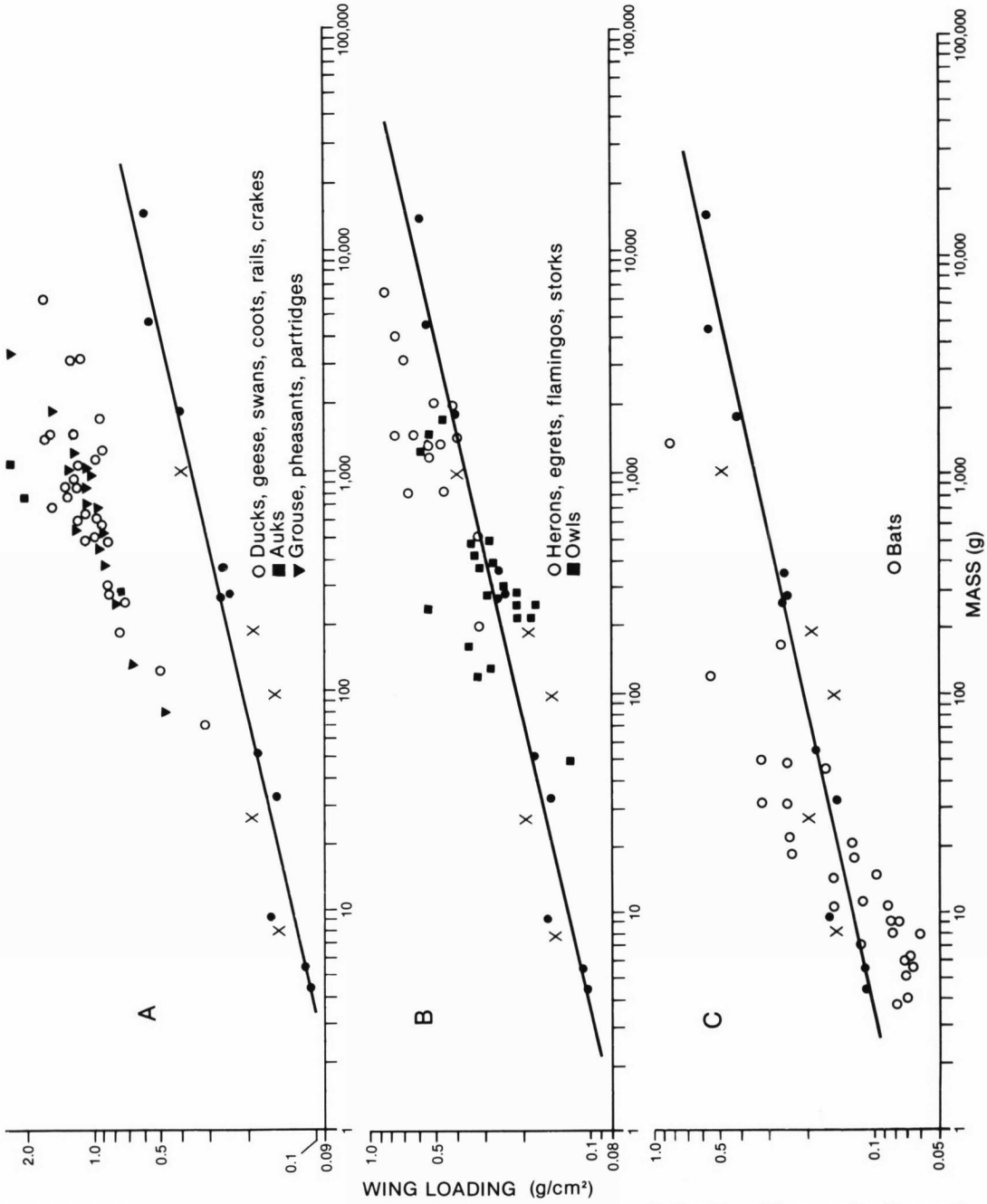
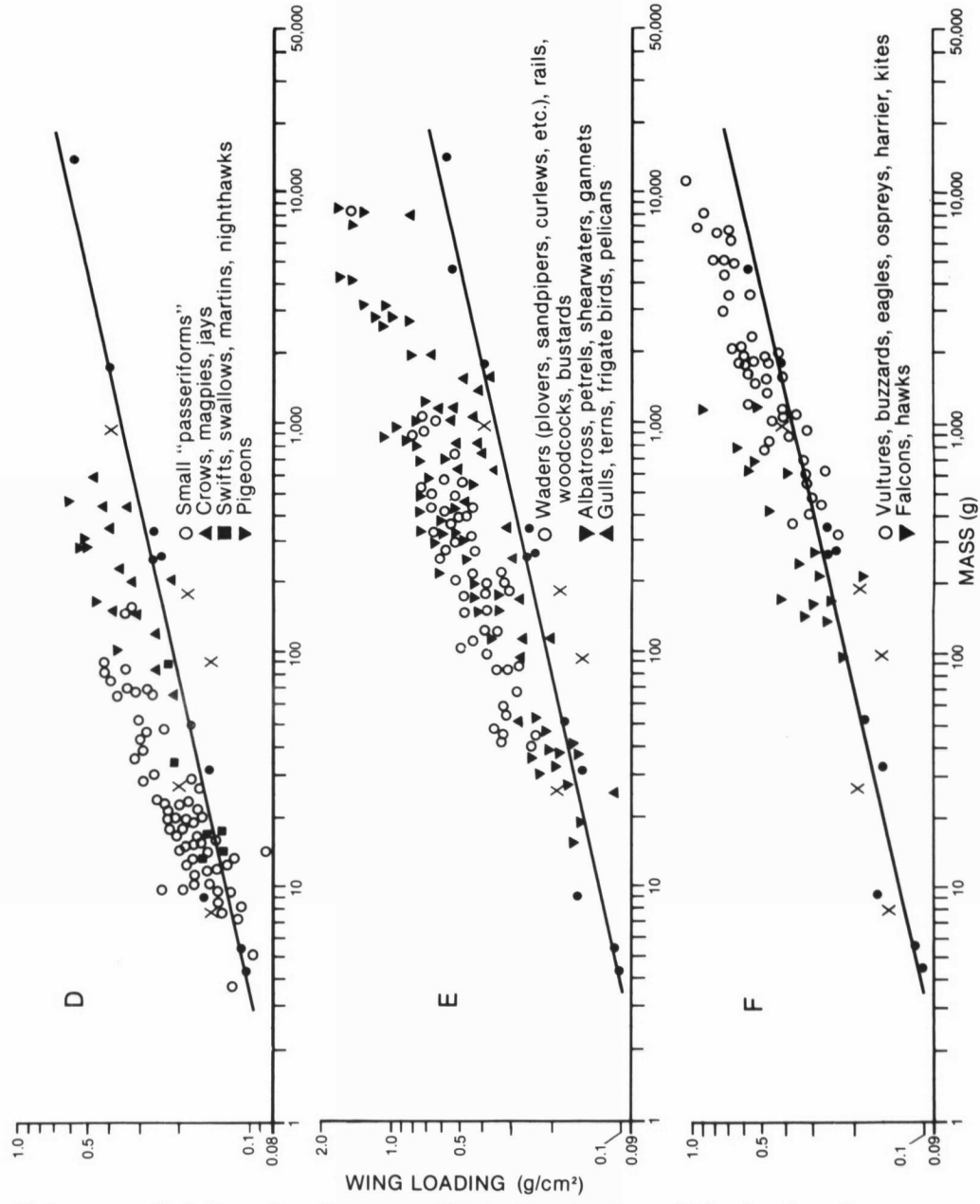


Fig. 10. Plots of mass versus wing loading showing overlap between pterosaurs and other flyers. The regression lines are for pterosaurs; dots and crosses are pterosaurs. Virtually all data were compiled from Greenewalt (1962). Most of the groups of birds correspond to those of Magnan (Greenewalt, 1962, Table 15). The data are listed in grams and grams per square centimeter; conversion factors to kilograms and kilograms per square meter are 1,000 g is 1 kg, and 1.0 g/cm² is 10 kg/m². — A. Pterosaurs and heavily loaded birds such as gamebirds, ducks and auks. There is no overlap. — B. Pterosaurs and herons, etc., and owls. Owls are lightly loaded birds that overlap greatly with pterosaurs, although there are probably no ecological parallels between the two groups. There is also some intergradation between herons, egrets, flamingoes, and pterosaurs. These birds are principally flappers. The storks (mass 3-7 kg) are excellent soarers as well as efficient flappers. — C. Pterosaurs and bats. Much intergradation is present at small sizes, but the wing loadings of larger bats generally exceed those of pterosaurs. — D. Pterosaurs and actively flapping birds. Most overlap is confined to small sizes. Much intergradation is present between pterosaurs and swallows, swifts, etc.; these are the only birds within this group that have wing planforms similar to those of pterosaurs. — E. Pterosaurs, shorebirds and seabirds. The high aspect-ratio wings of most of



these birds are generally similar to those of pterosaurs. Wing loadings of waders are higher than those of pterosaurs; most waders are active flappers that do little gliding or soaring. The wing loadings of pterosaurs are lower than those of fast soaring birds such as the albatross, shearwaters, gannets and large petrels. Small petrels (mass 15-54 g) have wing loadings that are about the same as in pterosaurs. Small petrels are basically flappers, although they will glide given proper wave sizes and windspeeds; these animals are common wave-soarers; when "water walking" with motionless wings the feet are creating "thrust" and this is not a form of soaring. The best match with respect to wing loadings is between pterosaurs and the more lightly loaded birds such as gulls, terns, and the frigate birds. Large terns and gulls and also frigate birds are soarers, but smaller gulls and terns are mainly flappers that will glide and soar under the right conditions. — F. Pterosaurs and soaring landbirds. The wing loadings of many of the lightly loaded hawks, vultures, etc., fall within the range of pterosaurs, especially from mass of 100 g to about 2 kg. The larger hawks, vultures, etc., are mainly soaring birds although smaller harriers, kites, hawks, and falcons are excellent flappers. The wings of most of these birds have much lower aspect ratios than do wings of pterosaurs of the same mass.

subsequent calculations. As mentioned earlier, his estimate of wingspan for the smaller pterosaur from Texas, *Quetzalcoatlus* sp., is between 5.49 and 6.71 m.

At least some other allometric relationships differ between individual species and pterosaurs taken as a whole. The equation for body length versus approximate wingspan for *P. kochi* contrasts with those for *P. micronyx* and for all pterosaurs (Table 3). Allometric relationships within a species may or may not be valid for all pterosaurs.

The same phenomenon is probably characteristic of birds and many other flyers. Kokshaysky (1977) presented data on the square root of wing area (Y) versus the cube root of mass (X) for three species of hawks and obtained an exponent of 0.819 for all data pooled together. However, the exponents for data within a single species are lower and range from 0.592 to 0.666. The general rule is that wing parameters increase less rapidly relative to body size or mass in a single species than in a large series of species.

Stein (1975) noted the similarity of wing configuration between large pterosaurs such as *Pteranodon* and the large molossid bat *Eumops perotis,* which has a wing loading of 0.266 g/cm². Assuming that the bat and *Quetzalcoatlus northropi* had the same wing loadings, Lawson (1977 personal communication) estimated its mass at approximately 140 kg. This approach is invalidated by the fact that wing loadings increase in progressively larger bats. In a similar vein, we tried scaling up *Pteranodon,* the best-known large pterosaur, to find the mass and wing loading of a *Pteranodon* of the same size as the giant Texas pterosaur. This process assumes that the two animals had the same shape, although this is doubtless not the case (Lawson, 1975a). The humerus lengths of *Pteranodon* and *Quetzalcoatlus northropi* are 29 cm (Bramwell & Whitfield, 1974) and 52 cm (Lawson, 1975a), respectively. The ratio of the humerus lengths yields a scale factor of 52 ÷ 29 or 1.793 for a linear dimension. For areas and masses, the scale factors become 3.215 and 5.765, respectively. The mass, wing area, and wing loading of *Pteranodon* are taken at 14.94 kg, 2.530 m², and 0.5904 g/cm² (Table 4, specimen 27). Applying the humerus scale factors, the estimated mass and wing area of a *Quetzalcoatlus northropi* with the same shape as *Pteranodon* are 86.13 kg and 8.136 m² with a wing loading of 1.059 g/cm². Because the humerus alone may not yield an appropriate scaling constant, another factor, 1.645, was derived from the ratio of the wingspans of

Table 3. *Allometric Equations On Which Size Predictions for* Quetzalcoatlus northropi *are Based.*

Y	X	a	Exponent	Standard error	Correlation coefficient	N	Data set
Wingspan cm	Humerus length cm	22.19	1.012	------	-----	--	*Pteranodon* (Lawson, 1975b)
Wingspan cm	Humerus length cm	29.70	1.012	------	-----	--	Regression equation (Lawson, 1975b)
Wingspan cm	Humerus length cm	13.91	1.055	------	-----	--	*Pterodactylus antiquus* (Lawson, 1975b)
Wingspan cm	Humerus length cm	16.24	0.8787	------	-----	--	Birds (Lawson, 1975b; Greenewalt, 1975a)
Wingspan cm	Humerus length cm	14.34	1.095	0.02195	0.9968	18	*P. kochi* (Wellnhofer, 1970)
Wingspan cm	Humerus length cm	13.42	1.331	0.07076	0.9771	15	*P. micronyx* (Wellnhofer, 1970)
Wingspan cm	Humerus length cm	18.63	1.095	0.05253	0.9814	16	All pterosaurs (this paper)
Wingspan cm	Body length cm	8.384	0.9478	0.03207	0.9915	17	*P. kochi* (Wellnhofer, 1970)
Wingspan cm	Body length cm	7.468	1.129	0.06382	0.9814	14	*P. micronyx* (Wellnhofer, 1970)
Wingspan cm	Body length cm	7.258	1.129	0.05794	0.9787	16	All pterosaurs (this paper)
Mass g	Wingspan cm	0.002253	2.459	0.1068	0.9870	16	All pterosaurs (this paper)
Wing loading g/cm²	Mass g	0.07913	0.2156	0.01929	0.9483	16	All pterosaurs (this paper)

Quetzalcoatlus northropi and *Pteranodon* (11.43 and 6.95 m). Here the computed mass, wing area, and wing loading are 66.45 kg, 6.844 m^2, and 0.9710 g/cm^2. Observe that the wing loading using either the humerus or the wingspan factor is greater even though the shape remains constant. We have not used other pterosaurs to develop scale factors because of the much wider gap in size between such taxa and the large Texas pterosaur.

Another approach employs the least-squares equations for our data for all pterosaurs (Table 3) and the wingspan of 11.43 m given by Langston. First, 11.43 m was substituted into our equation for wingspan and mass, which resulted in a calculated mass of 74.54 kg. Next, this mass was inserted into the equation for wing loading versus mass, which gave an estimated wing loading of 0.8888 g/cm^2. The corresponding wing area is 8.386 m^2. Applying the same technique to the smaller pterosaur from Texas, *Quetzalcoatlus* sp. (wingspan 6.096 m), gives predicted figures of 15.89 kg mass, 0.6369 g/cm^2 wing loading, and 2.495 m^2 wing area. Even though the allometry for all adult pterosaurs may not be valid for the Texas pterosaurs, these estimates are similar to those derived from increasing the size of *Pteranodon,* and we believe that the values are reasonable. Of the two methods of estimating the masses of the Texas pterosaurs, we prefer the figures based on the allometric equations because these take account of the shape changes seen in progressively larger pterosaurs. Recently Langston (1981) suggested a mass of 86 kg for *Quetzalcoatlus northropi,* a figure which is quite similar to those derived from our computations. Campbell (personal communication, Feb. 1981; see also Campbell, 1980; Campbell & Tonni, 1980) estimated the mass of the largest flying bird, a Tertiary teratorn from Argentina, at about 80 kg; the most likely wingspan equals 6.4 m. This animal fits into the "passeriform" cateogry of Greenewalt (1975b). Thus it appears that the mass of the largest flying bird was quite similar to that of the biggest pterosaur.

Table 4. *Basic Aerodynamic Data for 16 Pterosaurs.* (Specimen numbers are from the section on measurement.)

Specimen number	Mass (g)	Wing area (cm^2)	Wingspan (cm)	Aspect ratio	Wing loading (g/cm^2)
1	1,026	2,089	133.0	8.468	0.4911
2	8.104	55.85	35.97	23.17	0.1451
4	27.19	142.9	37.45	9.812	0.1902
8	195.6	1,045	108.5	11.26	0.1872
10	100.9	664.5	84.10	10.64	0.1518
11	9.423	58.21	25.50	11.17	0.1619
12	33.80	222.5	55.47	13.83	0.1519
14	5.533	50.30	25.53	12.96	0.1100
15	54.68	302.4	57.85	11.07	0.1808
17	4.472	42.58	24.04	13.57	0.1050
18	358.4	1,402	140.9	14.16	0.2556
19	280.8	1,122	115.7	11.93	0.2503
20	269.0	1,027	117.2	13.38	0.2619
23	4,702	8,162	324.3	12.88	0.5760
25	1,856	4,505	272.3	16.46	0.4124
27	14,940	25,300	695.0	19.09	0.5904

ALLOMETRY AND FLIGHT PERFORMANCE

At present, the senior author is working on the quantification of the flight performance of pterosaurs, and the remarks given here should be regarded as general and preliminary (see Brower, 1980). The critical relationship for a flying organism is wing area versus mass. In gliding, the wing area must be large enough to generate enough lift to support the mass and to ensure both a reasonable glide angle and moderate flight speeds. If the wing area is too small relative to mass, the gliding performance will approach that of the average igneous rock. This relation is also limiting for powered flight, during which both lift and thrust are developed by the flapping wing. The wing area must be sufficient to provide the necessary lift and thrust with a reasonable amount of muscle power. The concept of reasonable is important. Almost anything will fly, given enough power. A classic example is provided by rockets, which fly well with no lifting surfaces at all; the only aerodynamic surfaces on rockets are guidance fins. All thrust is derived from engines, but the cost of transport is extremely high in terms of power.

Probably the single most important parameter that controls the performance of low-speed aircraft is the wing loading; this is certainly true for flyers which have wings with the same general outlines or planforms and air-

foils.[1] The reason for this is readily explained for gliding. The basic aerodynamic equation is: $L = \frac{1}{2}\rho V^2 C_l S$. In the equation, L is the lift force, ρ is the density of air, V is the horizontal gliding speed, C_l is the lift coefficient, and S represents the wing area. For an animal gliding at a low angle, the lift force is approximately equal to the weight, that is, mass times the acceleration of gravity. If the weight is substituted for the lift force and the terms are rearranged, the horizontal flying speed is easily calculated from the following equation:

$$V = \sqrt{\frac{2mg}{\rho C_l S}},$$

in which m is the mass, and g the acceleration of gravity. The term m/S represents the wing loading. The point to be made is that the horizontal speed is proportional to the square root of the wing loading. Consequently animals with higher wing loadings will fly faster. Their higher flying speeds are typically gained at the expense of maneuverability (for example, see Vaughan, 1970a, b on bats). At least on an average basis, flyers with larger wing loadings also have faster vertical or sinking speeds. In similar fashion, wing loadings also dictate power requirements for flapping flight. The higher the wing loading, the faster the sinking speed, and the greater the necessary power output.

With this background, the conclusions to be drawn from the allometric relations between wing area, wing loading, and mass become clear. The negative allometry of wing loading with respect to mass and the positive allometry of wing area versus mass minimize the wing loadings of pterosaurs at all body sizes within the basic limits of geometry and functional morphology. It should be stressed that limits exist at both ends of the wing loading spectrum for animal flyers in this range of body sizes.

Wing loadings that are too high impose excessive flight speeds and power requirements. Long takeoff runs are characteristic of heavily loaded birds, such as the Canada goose, and aircraft. Bats are adapted for slow and highly maneuverable flight. The largest bat known to us has a mass of 1.6 kg and a wing loading of about 1.0 g/cm^2. Perhaps this wing loading limits this style of flight because higher wing loadings would cause faster flying speeds and lower maneuverability. The large exponent for wing loading versus mass in bats indicates that high wing loadings are reached at a small mass. Comparable wing loadings are not seen in pterosaurs below a mass of roughly 75 kg. Most birds fly more rapidly and are less maneuverable than bats. (We will intentionally ignore hummingbirds because their hovering or helicoptering flight is more similar to that of insects than most birds; see Kaufmann, 1970; Greenewalt, 1975b; Lighthill, 1975, 1977.) The maximum wing loadings of birds are those of grouse and auks, which equal about 2.4 g/cm^2. It is well known that most large flying birds, such as condors, bustards, and the albatross, are marginally powered (see Pennycuick, 1960 and McGahan, 1973 for two specific examples). Lighthill (1975, 1977), Pennycuick (1972a, 1975) and many others have suggested that most large birds are close to an upper limit for the power available relative to the power required. Bramwell and Whitfield (1974) calculated that *Pteranodon,* the best known large pterosaur, is also marginal with respect to power. Previous discussion indicates that the wing loadings of pterosaurs are lower than those of most birds and bats of the same mass. However, it is important to observe that pterosaurs are well within the entire range of wing loadings for birds and bats (Fig. 10).

Conversely, unusually low wing loadings would produce flyers with extremely slow flight velocities which could not fly or glide in the presence of even light winds and air currents. For example a hang-glider with the wing area of the smallest pterosaur would have a wing loading of less than 0.01 g/cm^2. An organism with a mass of 4 g and so low a wing loading would blow away in the slightest wind because the flying speed and wing loading would be too low to provide adequate performance. Another limit to minimum wing loadings may be the strength of the animal; it must be strong enough to withstand the stresses imposed by the loads developed during flight.

The data also suggest a general picture for the flight of pterosaurs. The low wing loadings indicate that the flying speeds of pterosaurs are slow compared to those of most other flying animals of the same mass. Generally, slow flying speeds are correlated with high maneuvera-

[1]The reader who is not familiar with aerodynamics should consult one or more of the following texts: Dommasch, Sherby, and Connolly (1961) on full scale aircraft, Simons (1978) for model airplanes, and Alexander (1968, 1975), and Pennycuick (1972a) on organisms. The review articles by Lighthill (1975, 1977) on the aerodynamics of flying animals and the relations between size and flight performance are especially informative.

bility, so we also believe that pterosaurs were probably quite agile and maneuverable when in the air (see Brower, 1980).

Pterosaurs and "passeriform" birds exhibit the widest range of masses known in flying animals. The approximate mass range of pterosaurs is 4.47 g to about 75 kg; of flying birds excluding hummingbirds, 3.8 g to roughly 80 kg; and of bats, 3.6 g to 1.6 kg. Obviously, marked negative allometry of wing loading relative to mass is a prerequisite to the development of a large flying organism. A low rate of increase of wing loading permits the animals to retain low wing loadings into large body sizes. Low wing loadings are necessary because a large flying organism must have a reasonably low flying speed, an adequate amount of maneuverability, and a tolerable power requirement. Both the "passeriform" birds and pterosaurs show roughly the same amount of negative allometry of wing loadings with respect to mass. On the average, the wing loading of a pterosaur is less than that of a "passeriform" with the same mass owing to the lower initial intercept of the equation for wing loading versus mass.

Another important factor for pterosaur flight is the aspect ratio, which is positively allometric compared to mass. The wings of larger pterosaurs have higher aspect ratios that generate smaller coefficients of induced or vortex drag than in the smaller taxa. Thus, larger pterosaurs are aerodynamically more efficient than small ones, at least in this respect.

SUMMARY AND CONCLUSIONS

Pterosaurs are fascinating flying animals because they exhibit a large range of body sizes. Known masses vary from about 4 g to 14.9 kg in *Pteranodon ingens*. The estimated mass of *Quetzalcoatlus northropi* is 75 kg. Although a comparable range of masses is known in "passeriform" birds, other birds and bats are much smaller. Large pterosaurs are typically visualized as gliders and soarers somewhat similar to large birds like frigate birds, vultures, and condors, with marginal amounts of power for takeoff and flapping flight (see Bramwell & Whitfield, 1974). Small pterosaurs probably had ample reserves for powered flight. Once in the air, small pterosaurs probably flew by active flapping, perhaps with intermittent gliding and soaring (Brower, 1980). Similar flight styles are known in birds (Kaufmann, 1970; Pennycuick, 1972b) and bats (Vaughan, 1970a, b).

Analysis of the size and shape of adult pterosaurs with the bivariate allometric equation of Huxley (1932) shows substantial changes in shape that are correlated with size. The shaft diameters of the wing and leg bones have marked positive allometry relative to mass, a direct reponse to problems of support. The slowest rates of increase are at the proximal and distal extremities of the wing. The entire gradient is adaptive with respect to aerodynamics and the distribution of loads applied during flight.

The two suborders of pterosaurs, the Rhamphorhynchoidea and Pterodactyloidea, are separated by contrasting patterns of allometry in the tail and one of the wing bones. Rhamphorhynchoids developed relatively long tails and comparatively short metacarpals, whereas the reverse is observed in pterodactyloids. The morphological differences in the tail probably reflect different flying habits in the two groups. The rhamphorhynchoids' long tail probably functioned to provide stability and aerodynamic control. The short tails of pterodactyloids imply less stability and a higher degree of maneuverability, like many bats, which are also short-tailed.

Of all the flyers studied, pterosaurs and "passeriform" birds are characterized by the highest amount of positive allometry of wing area relative to mass. The wing area is augmented rapidly with increasing body size in progressively larger animals. This relationship dictates that wing loading, i.e., mass per unit wing area, is strongly negatively allometric with respect to mass, so that wing loading rises slowly with larger mass. Inasmuch as the wing area provides the lift to support the mass during flying, this situation is a direct response to the problems of flight. Both "passeriforms" and pterosaurs show roughly the same exponent for wing loading versus mass. However, the initial intercept of the pterosaurs is lower, and on the average, pterosaurs have lower wing loadings than "passeriforms" of the same mass (Figs. 9, 10). The wing loadings of "shorebirds," "ducks," and bats increase with size much more rapidly than those of pterosaurs and "passeri-

forms." The negative allometry of wing loading relative to mass in conjunction with initially small wing loadings provides considerable insight into the flight performance and large range of body sizes observed in pterosaurs. Flying speeds, especially horizontal speeds, are typically proportional to wing loading. The initially low wing loadings and negative allometry of wing loading with respect to mass allowed pterosaurs to retain low wing loadings into a region of large body sizes. Owing to their relatively low wing loadings compared to those of most other flying animals, large pterosaurs flew slowly and maneuverably (e.g., Brower, 1980).

Wing loading is one of the most important parameters involved in low speed aerodynamics. The comparison of plots of wing loading versus mass for pterosaurs and other flyers suggests some analogies for the flight of these reptiles. Small pterosaurs have wing loadings approximately the same as those of small bats and birds, and all three groups are reasonably interpreted as active flappers. The wing loadings of pterosaurs such as *Nyctosaurus, Pteranodon ingens,* and some smaller taxa overlap with those of such lightly-loaded soaring birds as frigate birds and some vultures, and we infer that some parallel features of flight performance exist between these groups. The wing loading of *Quetzalcoatlus northropi* is about equal to that of a high-performance hang-glider such as one of the Princeton sailwings or a Rogallo-wing with a high aspect-ratio. Study of these hang-gliders may reveal some information about the flight of the largest pterosaurs.

Excessively high or low wing loadings probably limit the maximum size of a flying organism. If the wing loadings are too small, the flight speeds would be too low to permit flight in other than still air. Unduly large wing loadings cause problems such as long takeoff runs, high flight speeds, low maneuverability, and excessive power requirements. Pennycuick (1972a, 1975) noted that most large birds are marginally powered. Although the wing loadings of pterosaurs are lower than those of most birds and bats of the same mass, it is notable that the wing loadings of pterosaurs are still within the total range of wing loadings known in birds and bats (Figs. 9, 10).

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